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THE SHALLOW-WATER HERMIT CRABS OF FLORIDA[1]

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ABSTRACT

Twenty-three spp of pagurid crabs from the tidal and immediately subtidal waters of Florida, including one new sp., *Pagurus miamensis*, are described, illustrated and discussed and keys are presented for their determination. *Pagurus floridanus* (Benedict) is synonymous with *Pagurus pollicaris* Say. Both *Pagurus pollicaris* and *Pagurus longicarpus* have disjunct ranges, southern Florida separating what are probably subspecific populations of each. *Paguristes anomalus* Bouvier, *Pagurus pygmaeus* (Bouvier), and *Pagurus brevidactylus* (Stimpson) are reported for the first time from Florida and the U. S.

INTRODUCTION

With the growth of south Florida as a center of marine research, a more extensive knowledge of the local fauna has become imperative. Some of the most interesting but poorly known crustaceans of this area are the pagurid crabs. The systematic papers describing the hermit crabs of Florida shallow waters are numerous but very scattered and often inadequate for effective use by others than specialists in the group. To facilitate accurate determination of the species which occur intertidally and immediately below low-water mark, the task has been undertaken of bringing together previous information, supplementing it by collecting, redescribing the species found, illustrating them and constructing keys for their determination. One hitherto undescribed species is presented, and a number of nomenclatural problems have been resolved.

The author's sincere thanks are given to many of his fellow students at the University of Miami who collected much of the material dealt with in this study, and to his wife whose cheerful encouragement has facilitated the completion of the paper. He wishes to thank most

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warmly Dr. Elisabeth Deichmann, Curator of Marine Invertebrates at the Museum of Comparative Zoology at Harvard, for having given him access to the collection there. A number of difficult problems were solved with the help of Dr. Fenner A. Chace, Jr., Curator of Marine Invertebrates at the United States National Museum, who was kind enough also to read the manuscript. He is most grateful indeed to Dr. Frederick M. Bayer of the National Museum for the day of March 30, 1958. Much valuable advice was supplied by Dr. Jacques Forest of the National Museum at Paris. Dr. H. E. Gruner of the Humbold-Universität Zoologisches Museum at Berlin provided information regarding type collections there, for which he is grateful.

Mr. Marvin L. Wass of the University of Florida has offered numerous comments and has supplied comparative material, for which he would like to thank him. He is indebted also to Mr. Harvy R. Bullis, Jr. of the Fish and Wildlife Service at Pascagoula, Miss., for allowing him to examine shallow water specimens taken by the *Silver Bay,* and to Dr. John M. Teal of the University of Georgia for supplying him with comparative material of several species. He would like to thank especially Dr. Gilbert L. Voss, Curator of Marine Invertebrates at the University of Miami Marine Laboratory, for his guidance in this undertaking.

Methods

A search of the literature was made and collections in the USNM, MCZ, and UMML examined for Florida specimens. Extensive collecting was done in the south Florida region, but reefs were not as well collected as other habitats. The term "shallow water" as used here includes the intertidal zone and waters immediately below low water which can be explored by persons wading or skindiving. This area yields the greater part of all hermit crabs collected by students or normally obtainable for laboratory uses.

Because of the need for using technical terms in a taxonomic study such as this, a glossary is included in the section titled "Terminology."

Original drawings of all species treated are included, and some of these are the only known illustrations of the species.

Generic descriptions are in most cases modified from Alcock (1905). Because of the extensive synonymies listed for each genus by Alcock, in most cases only the original and the more important subsequent authors are here given.

Forest (1958) in a list of corrected names for French genera and

species also indicated the correct dates of their original publication and insofar as his data apply, the corrected forms have been used herein.

Size data are intended only as approximate indications of medium-large specimens. In most instances they represent the sizes of the largest individual of each sex examined by the author, and not necessarily the largest size attained by the species.

Historical Resume

Ives (1891) summarized most of our knowledge of the pagurids of the Florida area up to 1890. The first important writer on American crustacea was Say, who in 1817 listed a number of West Indian forms and two hermit crabs which extend in range from New England to Florida. Gibbes (1850) described a number of crustaceans from this area, including one hermit crab. De Saussure (1858) and Stimpson (1862) each made important contributions, describing a considerable number of pagurids. The deep water hermits of the Straits of Florida were discussed by Milne-Edwards and Bouvier who reported on the BLAKE collections.

Ives himself described a new species, *Clibanarius formosus,* from Yucatan in 1891. Actually Saussure (1858) had already described it under the name of *Pagurus cubensis* and perhaps Herbst (1796) before that was dealing with the same species when he described *Cancer sclopetarius.* Ives did not mention its occurrence in Florida but he did mention *Clibanarius vittatus,* taken at Little Gasparilla Pass and in addition recorded *Eupagurus pollicaris* (Say) from 9 to 12 feet of water off Manatee River in Tampa Bay, and *Eupagurus annulipes* Stimpson at Anclote Bay.

Three minor faunal papers appeared shortly after Ives, in which hermit crabs from nearby areas were listed. Rathbun (1897) recorded three species from Jamaica. *Coenobita diogenes* (Latreille), *Petrochirus bahamensis* (Herbst), and *Clibanarius sclopetarius* (Herbst). Rankin (1898) found two of the same species in the Bahamas and included several doubtful identifications. Two years later the same author recorded *Coenobita diogenes* (Latreille), *Calcinus tibicen* (Herbst), and *Clibanarius tricolor* (Gibbes) from Bermuda waters.

The next major paper dealing with the hermit crabs of the West Indian province was by Benedict in 1901, who listed 21 species from the waters of Puerto Rico. Ten of these are deep water forms, but all 11 shallow water species were taken during the present study. Descrip-

tions, some illustrations, and a key to the species of *Paguristes* of Puerto Rico were also included in this useful paper.

While Alcock's 1905 *Catalogue of Decapod Crustacea in the Indian Museum* is not concerned with our faunal area, the portion of his work dealing with pagurids is extremely useful, as it discusses hermit crabs generally, lists all species known to him at that time, world-wide, along with the distribution of each, and includes a world-wide key to the recognized genera.

Verrill (1908), reporting on the decapods of Bermuda, gave six species from those islands, four of which are common West Indian forms. The other two are questionable species of *Clibanarius, C. verrilli* (Rathbun) and *C. hebes* Verrill.

In 1918 two pertinent publications appeared. Bouvier listed from Cuba four species previously described and an additional three species found for the first time. Hay and Shore in their paper on the decapods of the Beaufort, North Carolina, region recorded eleven species of hermits, of which six were taken in waters deeper than those concerned here. All five of the shallow water species have been found in our waters.

Schmitt (1935) recorded seventeen species from the waters of Puerto Rico and the Virgin Islands of which five were deep water forms. Of the shallow water species, only *Paguristes depressus* was not found in the present study.

Wass (1955) reported nine species of hermit crabs from the waters of Alligator Harbor and vicinity in northwestern Florida. All of these, including his new species, *Paguristes hummi,* have been taken between Fort Myers and Miami. Since publication, Wass has also found *Paguristes puncticeps* Benedict (personal communication).

An indispensable paper for any systematic work with hermit crabs was published by Gordon (1956). This includes a bibliography of nearly all papers dealing with pagurids, systematic and otherwise, which have appeared since Alcock's 1905 monograph or which were not listed in the latter's references. In addition to listing papers by author, Gordon gives all names used for hermit crabs by all authors, without regard to synonomy, before and after Alcock. There are a few omissions.

Terminology

Because of the necessity of using a large number of technical words in a specialized report, the following partial list of commonly used

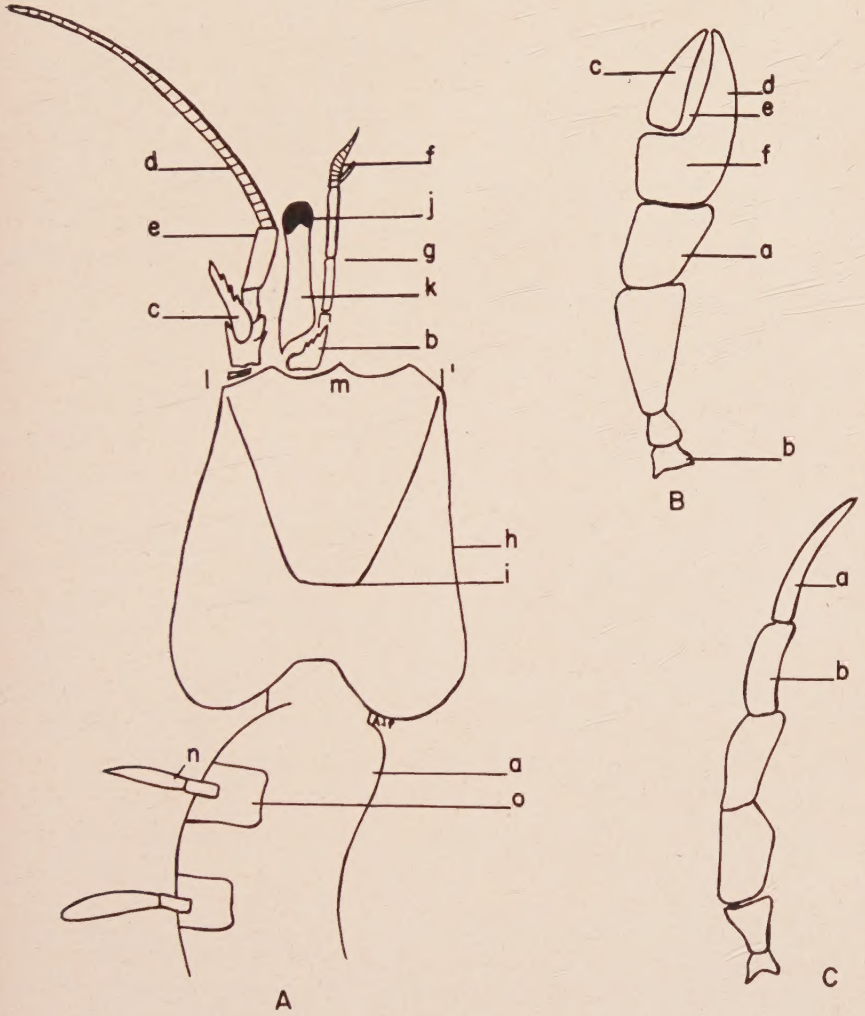

FIGURE 1. Diagram of external features of a hermit crab. A. Dorsal aspect of body: a. abdomen; b. ophthalmic acicle; c. antennal acicle; d. antennal flagellum; e. antennal peduncle; f. antennular flagellum; g. antennular peduncle; h. carapace; i. cervical suture; j. cornea; k. eyestalk (includes cornea); 1-1′. front; m. rostrum; n. pleopod; o. abdominal tergum. B. Parts of a cheliped: a. carpus; b. coxa; c. movable dactyl; e. hiatus; f. manus. C. A typical pereiopod: a. dactyl; b. propodus.

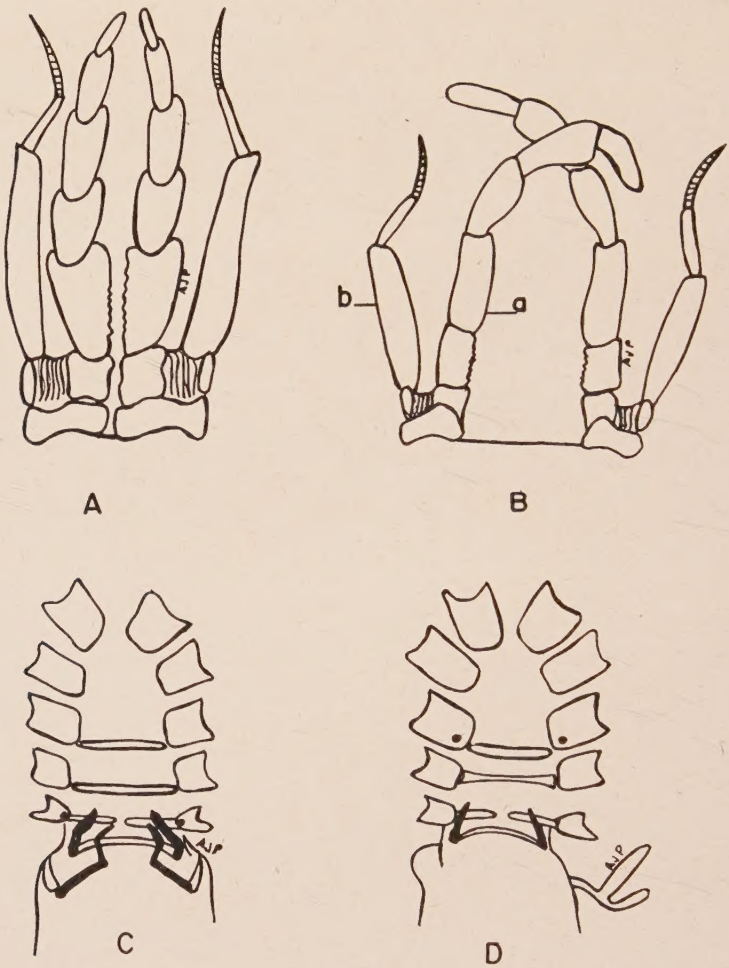

FIGURE 2. Above, illustration of relative proximity of third maxillipeds in (A) Diogeninae and in (B) Pagurinae; a. endopodite; b. exopodite. (Redrawn after Bouvier). Below, diagram of ventral surface of a typical *Paguristes* showing in black the position of the abdominal sexual appendages in (C) a male, and in (D) a female.

terms is included. Words not found in this list may be looked up if necessary in any of numerous textbooks on crustacean anatomy such as Storer (1951), Calman (1909), Bullough (1950), or in Jackson (1913). Figures 1A, 1B and 1C illustrate some of the most-used terms. Definitions are for pagurids only.

abdomen: the soft, coiled, posterior portion of the body (Fig. 1A. a).

acicle: a scale at the base of antennae or eyestalks (Fig. 1A. b, c).

ambulatory legs: the second and third pereiopods; the two pairs of appendages following the chelipeds.

antennae: the usually longer pair of jointed anterior appendages located laterally to the eyestalks (Fig. 1A. d, e).

antennules: the usually shorter pair of jointed anterior appendages located between and below the eyestalks (Fig. 1A. f, g).

approximated: very close together. See maxillipeds (Fig. 2A).

carapace: the chitinous shield covering the anterior portion of the body (Fig. 1A. h).

carpus: the wrist; third segment from the distal end of a pereiopod (Fig. 1B. a).

cervical suture: the groove separating the anterior and posterior portions of the carapace (Fig. 1A. i).

chelate: having a chela or pincer.

cheliped: the first pereiopod on either side bearing the claw (Fig. 1B).

cornea: the dark pigmented area at the tip of the eyestalk; the eye (Fig. 1A. j).

coxa: the appendage segment which articulates with the body (Fig. 1B. b).

dactyl (-us): the last segment of a pereiopod; the finger (Fig. 1B, c, d. Fig. 1C. a).

distal: farthest from the body, as opposed to proximal or close to the body.

endopod: the inner or medial of the two branches of a typical crustacean appendage (Fig. 2B. a).

eyestalk: elongate anterior appendage bearing the cornea (Fig. 1A. k).

exopod: the outer of two branches of a typical crustacean appendage (Fig. 2B. b).

flagellum: segmented, distal, whip-like portion of an antenna or antennule (Fig. 1A. f, d).

front: the entire width of the anterior margin of the carapace (Fig. 1A. 1-1′).

hiatus: a space, as between two fingers (Fig. 1B. e).

L. c.: length of carapace measured from tip of rostrum to transverse margin of posterior carapace between membranous lobes.

manus: the hand; the modified propodus of a cheliped (Fig. 1B. f).

maxillae: either of two pairs of appendages immediately posterior to the mandibles and preceding the maxillipeds.

maxillipeds: any of three pairs of appendages posterior to the maxillae and preceding the chelipeds or first pereiopods. (For third maxillipeds, see Figs. 2A, 2B).

merus: the segment proximal to the carpus.

obsolete: indistinct; imperfectly developed.

ophthalmic: ocular; pertaining to the eye.

peduncle: a supporting, stalk-like portion of an appendage (Fig. 1A. e, g, k).

pereiopods: any of five pairs of thoracic appendages.

pleopods: the abdominal appendages, usually unpaired in pagurids, used in the female for egg-carrying (Fig. 1A. n).

propodus: segment preceding the dactyl; the manus of a cheliped (Fig. 1B. f.; Fig. 1C. b).

pubescent: hirsute; covered with hairs.

rostrum: the median projection of the front (Fig. 1A. m).

setae: bristles or hairs.

subchelate: imperfectly chelate, ending in a terminal hook which bends down on the segment to which it attaches.

subequal: almost equal in size.

sulcus: a groove.

tergum: a protective plate on the abdomen (Fig. 1A. o).

Classification

A general classification of the hermit crabs and closely allied forms is given below. It is taken from Calman (1909) who gave good descriptions of the higher categories, and who is generally accepted as an authority on the higher classification of the Crustacea.

Phylum ARTHROPODA

Class *CRUSTACEA*
Subclass MALACOSTRACA
Series EUMALACOSTRACA
Division *EUCARIDA*
Order DECAPODA
Suborder REPTANTIA
Section ANOMURA
Tribe *PAGURIDEA*
Family PYLOCHELIDAE
Family PAGURIDAE
Family COENOBITIDAE
Family LITHODIDAE

Calman's description of the tribe Paguridea is as follows:

> Abdomen nearly always asymmetrical, either soft and twisted or bent under thorax; rostrum generally small or absent; first legs chelate; tail fan not typical, uropods (when present) adapted for holding the body into hollow objects.

The following description of the Family Paguridae has been translated by the writer from Bouvier (1940) who included the Coenobitidae in the Family Paguridae, contrary to the opinion of previous authors.

> Abdomen asymmetrical, at least in the uropods and ordinarily also in the pleopods (numbers 2 to 5 or 3 to 4) which ordinarily are developed only on one side, usually the left. Carapace progressively enlarged towards the posterior, membranous on the sides where very thin lines lay out a network there, ordinarily limited above by the *ligne anomurienne*. The basal article of the ocular peduncle developed dorsally in a triangular scale (the ophthalmic acicle). Thoracic sternites corresponding to the third, fourth, and fifth legs free and mobile, legs four and five reduced and modified. The middle terga of the abdomen separated more or less by the membrane.

A more recent paper by MacDonald, Pike, and Williamson (1957) presents a revised classification of the families, superfamilies, and subfamilies of the pagurids. This new classification, reproduced below, is based on a study of larval characters of ten species of British pagurids. The superfamilies are separated on the rather fundamental character of relative proximity of the third maxillipeds. There is much to be said for this system and it is likely to be widely accepted when further work provides additional evidence in favor of it. For the present, however, the more traditional grouping will be used.

Superfamily *COENOBITOIDEA* (= Paguridea
Serie Pagurienne Bouvier, 1940)

Family PYLOCHELIDAE Bate, 1888
Family DIOGENIDAE Ortmann, 1892 (subfam.) emend. (= subfams. Pagurinae — Diogeninae Ortmann, 1892, = subfam. Dardaninae Schmitt, 1926)
Family COENOBITIDAE Dana, 1852
Family LOMISIDAE Bouvier, 1894
Superfamily *PAGUROIDEA* (= Paguridea Serie Eupagurienne Bouvier, (1940)
Family PAGURIDAE Latreille, 1802-3 (*fide* Forest & Holthuis, 1956) emend. nobis (= subfam. Eupagurinae Ortmann, 1892)
Family LITHODIDAE Leach ms. in Samouelle, 1819 (*fide* Dr. I. Gordon, pers. comm.)

The families Diogenidae and Paguridae of the above classification have long been considered subfamilies and the nomenclature of the two groups, whether they be considered subfamilies or families, has been closely involved with several long-confused generic names. A word on this seems in order.

The problem has been discussed in detail by Walton and Stevens (1955) and by Forest (1958) and the International Commission on Zoological Nomenclature has ruled on the situation in Opinions 11 and 472. The generic name *Pagurus* Fabricius, 1775 with *Cancer bernhardus* Linnaeus, 1758 as type species has been placed on the Official List of Generic Names in Zoology, and *Eupagurus,* long used by some workers for that genus, is to be suppressed. In the opposite subfamily, the genus which also has sometimes been called *Pagurus* is hereafter to be recognized as *Dardanus* Paulson, 1875 (type: *Dardanus helleri* Paulson). The name of the subfamily containing *Pagurus* is Pagurinae. However, in the second group, to which both *Dardanus* and the genus *Diogenes* belong, the subfamily name Diogeninae Ortmann, 1892 has priority over Dardaninae Schmitt, 1926.

A KEY TO THE GENERA OF FLORIDA SHALLOW-WATER HERMIT CRABS

1. Antennular peduncles about 5 times the length of the eyestalks which are laterally compressed; antennular flagellum ends abruptly and bluntly; land hermits. Family Coenobitidae ..... *Coenobita*
   Antennular peduncles less than twice length of eyestalks which are not laterally compressed; antennular flagellum ends in a filament; marine hermits. Family Paguridae 2

2. Third maxillipeds widely separated at base by a sternum (Fig. 2B). Subfamily Pagurinae ..... *Pagurus*
   Third maxillipeds approximated (Fig. 2A). Subfamily Diogeninae 3
3. Paired appendages present on first two abdominal segments of male and on first segment only of female (Figs. 2C, 2D) ..... *Paguristes*
   No paired appendages on anterior abdominal segments of either sex 4
4. Chelipeds similar and subequal; fingers move horizontally 5
   Chelipeds dissimilar and unequal; fingers move obliquely or nearly vertically 6
5. Finger tips spooned; antennal flagellum long and not hairy .... *Clibanarius*
   Finger tips acuminate; antennal flagellum short and very hairy ... *Isocheles*
6. Chelipeds markedly unequal, left much larger than right 7
   Chelipeds not markedly unequal, right slightly larger than left .. *Petrochirus*
7. Major manus tuberculate, with appressed setae ..... *Dardanus*
   Major manus smooth, without hairs ..... *Calcinus*

Family Coenobitidae Dana, 1851
Genus *Coenobita* Latreille, 1826

Coenobita Latreille, 1826: 276. Alcock, 1905: 139.

Chelipeds unequal, left very much the stouter, all segments short, broad; fingers move vertically and have extreme tip corneous or calcareous.

Ambulatory legs stout, not extending much beyond major cheliped, if at all. Penultimate pair of legs subcheliform, dactylus minute and propodus forming large suboval plate. Last legs cheliform, not shorter nor much slenderer than preceding pair.

Carapace elongate, contracted and compressed anteriorly including all appendages, well calcified except on patches of posterior carapace or branchiostegites. Rostrum almost imperceptible.

Eyestalks and ophthalmic acicles juxtaposed, former compressed.

Antennular peduncles extremely long; flagella compressed, rigid, and truncated at tip, upper flagellum being much longer and broader than lower.

Antennal peduncles compressed, acicle small and often fused with second joint; flagellum long, coarse, not very flexible.

Tropical land hermits.

Coenobita clypeatus (Herbst, 1791)
Fig. 3

Cancer diogenes Catesby, 1771. Not *Cancer diogenes* Linn., 1758: 631.
Cancer clypeatus Herbst, 1791: 22, pl. 23, figs. 2a, 2b.
Pagurus diogenes, Latreille, 1811: 632, pl. 284, figs. 2, 3.
Cenobita diogenes, Benedict, 1901: 139.
Coenobita clypeatus, Rathbun, 1920: 329.
Coenobita clypeatus, Schmitt, 1935: 207, fig. 68.

Diagnosis. Antennular peduncles 5 times length of eyestalks; latter as long as front, laterally compressed; propodus of second left ambulatory leg flattened and smooth; inferior margin of dactyl and propodus a sharp serrate ridge of spiniform tubercles in dactyl and blunt tubercles or nodules in propodus.

Description. Chelipeds unequal, left much larger than right; tips of fingers of major manus calcareous, not spooned, while those of minor manus corneous, spooned. Both chelipeds covered on exterior surfaces with small raised points which become sharp black-tipped spines on undersides and along superior margin. On that margin these are distributed in two very even rows on each hand. Median side of each merus and carpus very flat and smooth. Long fine setae on minor cheliped.

Ambulatory legs all stout, largely covered by small black forward-pointing spines so that appendages feel smooth when brushed towards tips but rough when brushed towards body. Second left ambulatory leg broader or deeper than corresponding leg of right side.

Carapace elongate, anterior portion slightly longer than posterior. Wider by about 2 times at cervical suture than at front. Front concave with only suggestion of rostral projection.

Eyestalks only about 3 times longer than broad, flat on medial side with a depression on that surface of each eyestalk visible when latter are moved apart. Pair of ophthalmic acicles reduced, blunt, oval, touching each other.

Antennular peduncles extremely long, when extended, exceeding eyestalks by 4 times length of latter.

Antennal peduncles exceeding eyestalks by length of latter, originating below rather than beside the eyestalks, thus differing from true marine hermits.

Color. Left manus in adults blue to purple, with orange dactyls. Last segments of ambulatory legs orange. Young with purple and gray appendages, gradually acquiring orange pigment with age. Colors persistent in alcohol and formalin, but not present in three specimens preserved 25 years.

Size. L. c. male, 32 mm; female, 24 mm.

Range. Florida, Bermuda, West Indies to Venezuela.

Type locality. West Indies. See Discussion.

Type. No longer with Herbst's collection at Berlin, and believed destroyed.

Discussion. Rathbun (1920) gave as her reason for rejecting the name *diogenes* in favor of the *clypeatus* of Herbst, that *"Cancer diogenes"* was incorrectly applied to the animal discussed by Catesby which was apparently the *Coenobita* of the West Indies, but which does not fit the description of *Cancer diogenes* as given by Linnaeus. The name *Coenobita clypeatus* has been used by Latreille and many others (see Alcock, 1905: 142) for a Pacific form, but incorrectly. The original description by Herbst does not definitely indicate with which species

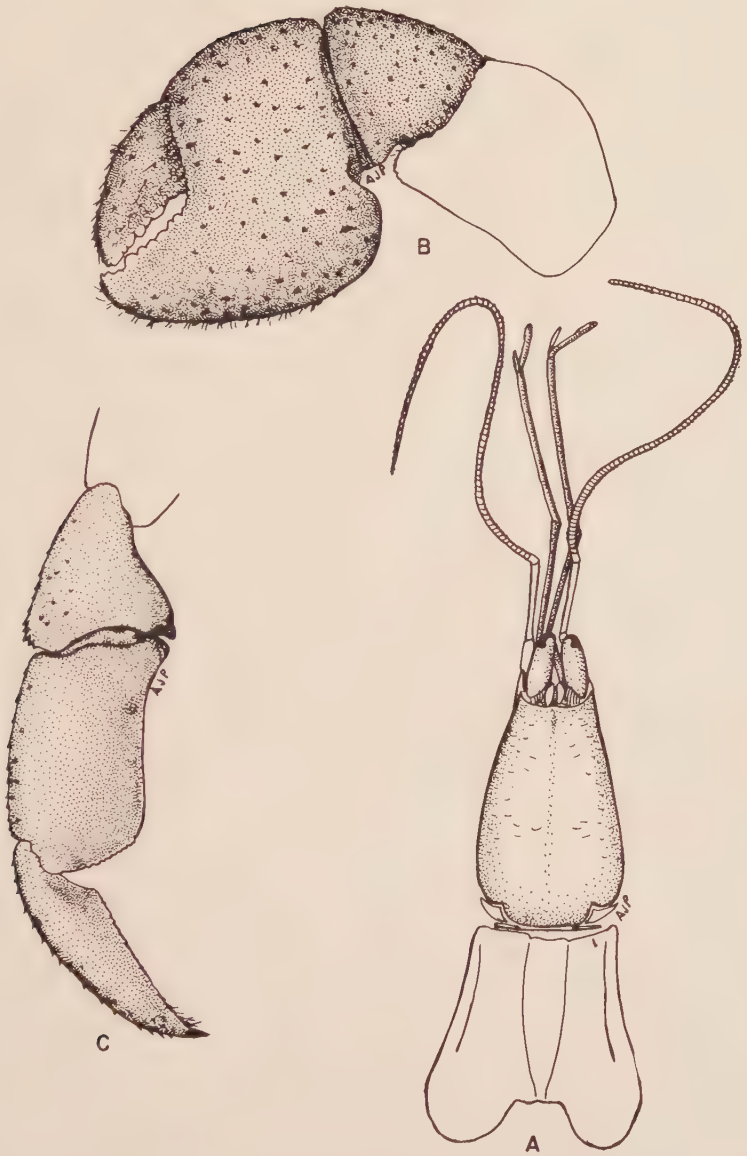

FIGURE 3. *Coenobita clypeatus* (Herbst, 1791), x 1.5. A. Dorsal view of carapace. Note extremely long antennular peduncles. B. Left cheliped. C. Second left ambulatory leg.

he dealt and he gave the type locality as "East Indies." This, however, is apparently an error, as to quote Schmitt (1935),

> Hilgendorf, 1869, Von der Decken's Reisen in Ost-Afrika, III, p. 98, who has examined the specimen says that Herbst's type is the West Indian species.

Remarks. The Coenobitidae are typically terrestrial in habit, but may be found at the shore at times of the year when the zoea are liberated into sea water and presumably copulation of adults takes places. The young, after a planktonic period like other pagurids, seek shells near the shore and as they grow can tolerate longer and longer periods of exposure to air, until as adults they may be found in woods and on hills some disance away from the beaches.

Material. Florida: 3 juv. females; from beach at Bear Cut, Key Biscayne, 8 Oct. 1958, student field class.

4 juv.; Indian Key, 1 Feb. 1958, Provenzano.
1 male and 1 female; Key Largo, 1933, UMML 32:323 & 32:320. Collector unknown.
Puerto Rico: 1 male; Culebra, 7 Nov. 1957, C. Feliciano.

Family Paguridae Latreille, 1802-03
Sub-family Diogeninae Ortmann, 1892

This subfamily is characterized by having the *third maxillipeds approximated* at the base. Alcock, who used the name Pagurinae for this subfamily, also gave as characteristic that

> the chelipeds are equal, or subequal, or the left is vastly the larger; very rarely is the right slightly, never is it vastly larger than the left.

The majority of genera of hermits in Florida inshore waters belongs to this group.

Genus *Calcinus* Dana, 1851

Calcinus Dana, 1851: 456; Stimpson, 1859: 234; Alcock, 1905: 51.

Chelipeds unequal, left the larger; fingers move obliquely or vertically; finger tips calcareous, spooned.

Fourth pair of pereiopods subchelate, 5th pair chelate.

Carapace elongate, anterior portion very firmly calcified, but posterior flaccid. Rostrum small but very distinct.

Eyestalks long and slender, ophthalmic acicles slender and approximated.

Antennal flagellum non-setose. Acicle well formed, usually short.

Exopods of all three pairs of maxillipeds flagellate. Endopod of first maxillae with small recurved flagellum.

Bouvier (1940) and Alcock (1905) mention the close relationship of *Calcinus* to *Clibanarius*, the former differing from the latter chiefly in the form of the chelipeds and the denser texture of the hard parts of the exoskeleton. Hard parts are densely porcellanous in texture and, as a rule, are vividly colored. The genus is tropical and subtropical in distribution. Until recently only one species was known to occur in the West Indies, but there is evidence of another at Bermuda and perhaps elsewhere to the south (Provenzano, in press).

Calcinus tibicen (Herbst, 1791)

Fig. 4

Cancer tibicen Herbst, 1791: 25, pl. 23, fig. 7.
Pagurus sulcatus Milne-Edwards, 1836: 279.
Calcinus sulcatus, Benedict, 1901: 141, pl. 5, figs. 3, 3a. Verrill, 1908: 439, text figs. 56, 57, pl. 28, fig. 7.
Calcinus tibicen, Schmitt, 1935: 198, figs. 60a, 60b.

Diagnosis. Hard parts porcellanous, not setose. Propodus of second left ambulatory leg wider than right counterpart, with longitudinal groove laterally. Eyestalks longer than front.

Description. Chelipeds unequal, left much larger than right. Fingers move obliquely, tips calcareous and acuminate. Both chelipeds devoid of spines and setae.

Ambulatory legs smooth, tufts of setae on inferior margins of dactyls. Propodus of second left ambulatory leg wider than those of other legs, and with a wide longitudinal groove on outer surface. See "Color."

Carapace with anterior portion longer than wide. Triangular projection in advance of lateral projections. Punctae on anterior portion light.

Eyestalks slender, curving gently outward, slightly exceeding in length the width of front. Ophthalmic acicles acute, terminating in one or two spines.

Antennular peduncles reach to non-pigmented portion of eyestalks.

Antennal peduncles reach to about last third of eyestalks. Acicle armed with 5-7 white-tipped spines.

Color. Chelipeds red-brown to maroon, often tinged with purple, but fingers white-tipped. Dactyls of ambulatory legs white or yellow, banded with red. Distal ends of propodi also light. Eyestalks orange-red, becoming white before cornea. Carapace usually a rich red, often tinged with purple, more rarely with green, and bearing white punctae. In very young specimens most of carapace, except immediately behind front, lacks intense color. Colors persistent in alcohol and formalin, longer in the latter.

Size. L.c. male, 12 mm; female, 12 mm.

Range. Bermuda, West Indian region from south Florida to Brazil.

Type locality. Not given by Herbst.

Type. No longer with Herbst's collection at Berlin, and believed destroyed.

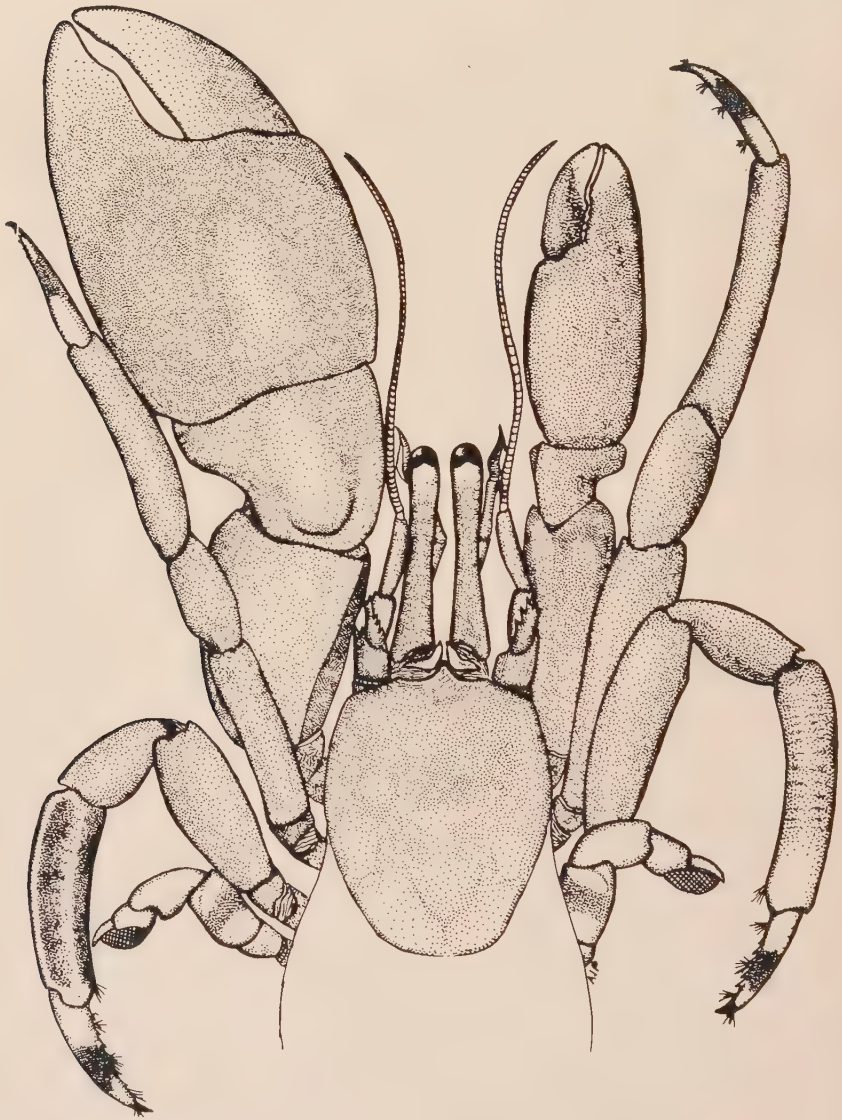

FIGURE 4. *Calcinus tibicen* (Herbst, 1791), x 4. Note grooved propodus of second left ambulatory leg.

Discussion. In this case, as in that of *Coenobita clypeatus* (Herbst, 1791), a Pacific species carried for some time a name properly belonging to a West Indian hermit. Herbst's original description of *Cancer tibicen* clearly indicates the presence in his species of the grooved propodus of the second left ambulatory leg. Yet Milne-Edwards (1836) and others after him applied the name of *tibicen* to a Pacific species without this diagnostic character, and the West Indian species was named by Milne-Edwards as *Pagurus sulcatus.* Herbst's name is correctly applied only to the West Indian species.

Alcock (1905: 164) listed Ecuador as a part of the range of this species, but this is probably an error.

Remarks. This species is often taken in rocky habitats in company with *Clibanarius tricolor* even high in the intertidal zone. Schmitt says it is found to a depth of 18 Fathoms.

Material. Florida: 2 ovig. females and 4 males; Ragged Key, 30 March 1957, Provenzano. One of females deposited as UMML 32: 934.

4 non-ovig. females and 3 males; Indian Key in rocky tide pools, 1 Feb. 1958. UMML 32: 1078. Provenzano.

1 male; Bear Cut, Biscayne Bay, 6 March 1958. John Klussman and Joe McMahon.

1 male; Bache Shoals, off Elliot Key, Aug. 1957. Raymond Manning.

1 ovig. female; French Reef, 12 April 1958. Gene Shinn.

2 males; Bear Cut, Biscayne Bay, 8 October 1957. Student field class.

Genus *Clibanarius* Dana, 1851

Clibanarius Dana, 1851: 461; Alcock, 1905: 40.

Chelipeds similar, equal or subequal, or one may be larger; fingers move horizontally; finger tips corneous, spooned.

Fourth pair of pereiopods subchelate, 5th pair chelate.

Rostrum distinct, but short.

Eyestalks long and slender; ophthalmic acicles well developed, usually closely approximated.

Antennal flagellum long, non-setose. Acicle usually short.

Three pairs of maxillipeds all with well developed flagellum on exopod. Endopod of first maxilla has a recurved flagellum.

Typically tropical, but also subtemperate in distribution, normally in shallow waters. Represented in Florida shallows by four species.

Key to the Florida Species of *Clibanarius*

1. Dactyls of ambulatory legs shorter than propodi 2
   Dactyls of ambulatory legs not shorter than propodi 3

2. Legs with broad longitudinal light stripe on dark background ... *antillensis*
   Legs without any longitudinal stripes, instead banded with orange at proximal ends of propodi and dactyls; dominant color blue ..... *tricolor*
3. Propodi with dark stripe laterally, bordered on each side by light stripe of similar width ..... *cubensis*
   Propodi with 4 thin light stripes laterally, separated by broad dark stripes ..... *vittatus*

Clibanarius tricolor (Gibbes, 1850)
Fig. 5A

Pagurus tricolor Gibbes, 1850: 189.
Clibanarius tricolor, Stimpson, 1859: 234; Schmitt, 1935: 200, fig. 61.

Diagnosis. Dactyls of ambulatory legs shorter than propodi; no longitudinal stripes laterally on ambulatory legs; transverse diffuse band of orange at proximal end of dactyl and of propodus of each leg, which except for white or yellow dactyl is otherwise blue.

Description. Chelipeds subequal, right slightly larger than left. Both hands with coarse spines on upper surface, each light in color, contrasting with background. Both chelipeds with sparse but long setae. Carpus with only 4-5 spines on upper surface.

Ambulatory legs with dactyls not longer than propodal joints. Second right leg longer than corresponding left leg. Scattered punctae on legs, with long but fine setae.

Carapace subquadrate in anterior portion. Rostrum in advance of lateral projections of front. Carapace smooth, punctate. Cervical groove almost a straight line across the carapace, anterior portion of which is longer than broad.

Eyestalks slender, curving gently outward, not longer than width of front. Left occasionally longer than right. Ophthalmic acicles approximated, with 4-5 teeth on anterior margins.

Antennular peduncles extend beyond cornea.

Antennal peduncles scarcely reach base of cornea. Acicles with about 6 spines on medial margin, one low on lateral margin, obscured by setae. Antennae reach well beyond chelipeds.

Color. Only *C. tricolor,* of the species of this genus known from Florida, lacks longitudinal stripes on the lateral surfaces of the ambulatory legs. In fresh material chelipeds brownish to black, with white spines. Dactyls of ambulatory legs black-tipped, white or yellow most of their length, then orange at proximal end. Proximal ends of propodi also orange, segments otherwise pale to dark blue. Carapace and eyestalks blue, antennae orange. In formalin colors persist some time, but in alcohol, the blue fades, leaving on ambulatory legs only orange bands and punctae and on chelipeds red-orange instead of brown.

Size. L.c. male, 9 mm; female, 6 mm.

Range. Bermuda, Florida from Miami through the keys, West Indies.

Type locality. Key West, Florida.

Type. Not traced.

FIGURE 5. *Clibanarius* leg color patterns. A. *C. tricolor* (Gibbes, 1850), x 10. B. *C. antillensis* Stimpson, 1862, x 10. C. *C. cubensis* Saussure, 1858, x 7. D. *C. vittatus* (Bosc, 1802), x 4.

Discussion. As Schmitt (1935: 199) has pointed out, one may have difficulty separating this species from *C. antillensis* Stimpson when the colors have disappeared, but when the patterns are present, there can be no mistake.

Remarks. The species may be very abundant in the intertidal zone, especially where there are rocks, and often under conditions too severe for other hermits. When exposed for any length of time as during low

tides, hundreds of individuals may congregate in patches recognizable from a distance. *Batillaria minima* is a favorite, but by no means exclusive shelter for this species. One habitat it does not particularly abound in normally is *Thalassia* beds. Although no material is listed below from Bear Cut, the species is abundant in some localities there.

Material. 1 non-ovig. female and 5 males; 12 mi. S. of Greyhound Key, 12 Oct. 1957, Raymond Manning.

3 ovig. females and 17 other specimens; Long Key, 3.5 mi. SW of Greyhound Key, Fla. Bay side, 27 Jan. 1958, C. R. Robins and W. R. Courtenay, Jr.

2 males; Crawl Key, 28 Jan. 1958, H. Kumpf. UMML 32: 1078.

23 males, 2 non-ovig. females and 70 other specimens, none ovigerous; rocky tide pools at Indian Key, 1 Feb. 1958, Provenzano.

9 ovig. females and 13 other specimens; S. end of Long Key on Ocean side, 19 April 1957, Provenzano.

8 ovig. females and 21 other specimens; Matheson Hammock, just S. of Miami, 20 April 1957. Provenzano.

1 ovig. female and 25 other specimens; north Key Largo, 12 May 1957. Provenzano.

18 specimens, none ovigerous; north Key Largo, 21 May 1957. Provenzano.

Clibanarius antillensis Stimpson, 1862
Fig. 5B

Clibanarius antillensis Stimpson, 1862: 85; Benedict, 1901: 142, pl. 6, fig. 1; Yap-Chiongco, 1938: 188.

Diagnosis. Dactyls of ambulatory legs shorter than propodi; single broad longitudinal light stripe bordered by olive or brown on lateral surface of last segments of ambulatory legs.

Description. Chelipeds subequal, right may be slightly larger. Coarse spines on hands as in *C. tricolor,* but relatively smaller. Manus and carpus sparsely hairy. Surface of merus pitted. Fingers of hands as in others of genus, corneous, spooned.

Ambulatory legs sparsely hairy, dactyls shorter than propodi. One or two spines on antero-dorsal margin of carpus of first ambulatory legs, one there on second pair. Second left dactyl and propodus somewhat flattened with dorsolateral ridge, but this also in preceding species.

Anterior carapace subrectangular, punctate. Rostrum triangular, in advance of lateral projections. Cervical suture almost a straight line.

Eyestalks longer than width of front, left may be longer than right. Ophthalmic acicles broad, approximated, armed with about 6 spines decreasing in size from medial.

Antennular peduncles exceed length of eyestalks or of right eyestalk.

Antennal peduncles vary in relative length between individuals, but may be as long as left eyestalk, or may fall short of cornea. Acicles armed with spines similar in number and arrangement to those in *C. tricolor.*

Color. In life, chelipeds olive to rusty brown with white spines, but white does not extend as far from the bases of the spines as in *C. tricolor.* Last three segments of ambulatory legs with broad white stripe

laterally with diffuse margins. Merus with 2 stripes. Eyestalks greenish blue. Antennular peduncle greenish blue with orange base, orange flagellum. Antennae orange.

Size. L.c. male, 9.5 mm; female, 9 mm.

Range. Southern Florida through West Indies to Curacao and Brazil. Also reported from the Philippines. (See Discussion.)

Type locality. Barbados.

Type. Not traced, but presumed lost.

Discussion. This species is closely related to *C. tricolor* from which, when the colors are completely gone, it can be distinguished only with difficulty if at all. Yap-Chiongco (1938) lists the West Indian *C. antillensis* as occurring in Philippine waters and describes his material in some detail. It would be of considerable interest to compare Pacific specimens with those from the West Indies, but I have been unable to do this as yet. He also lists, somewhat more doubtfully, another species of *Clibanarius* which might be the same as a West Indian species. So far as I am aware at this date, no other West Indian littoral hermits have been reported from the Pacific, although several have close relatives there and deeper water species are often cosmopolitan.

Remarks. This species is often taken with *C. tricolor* but does not appear to be as tolerant of intertidal conditions.

Material. 4 males and 35 other specimens; Matheson Hammock just S. of Miami, 27 Jan. 1958; Manning and Provenzano. Males deposited UMML 32: 1079.

23 Specimens; S. end of Long Key, ocean side, 19 April 1957, Provenzano.

9 ovig. females and 5 other specimens; Matheson Hammock, 20 April 1957, Provenzano.

12 males; 12 mi. S. of Greyhound Key, 12 Oct. 1957, R. Manning.

6 specimens; north Key Largo, 12 May 1957, Provenzano.

Clibanarius cubensis (Saussure, 1858)

Fig. 5C

? *Cancer sclopetarius* Herbst, 1796: 23, pl. 23, fig. 3.
Pagurus cubensis Saussure, 1858: 455.
Clibanarius sclopetarius, Stimson, 1862: 85; Benedict, 1901: 142.
Clibanarius formosus Ives, 1891: 182, pl. 5, figs. 1, 2.
Clibanarius cubensis, Rathbun, 1900: 144; Schmitt, 1935: 199.
? *Clibanarius sclopetarius,* Yap-Chiongco, 1938: 192.

Diagnosis. Dactyls of ambulatory legs not shorter than propodi. Latter with single median longitudinal dark stripe laterally, bordered by light stripe of equal width on either side.

Description. Chelipeds equal, sparsely hairy, covered with short spines, each pigmented darker than basic color of hands. Manus about 2 times longer than

broad, fingers more than half total length of hand. A large black-tipped spine on antero-dorsal margin of carpus. One spine on lower antero-lateral margin of merus, row of much smaller spines on lower medial margin.

Ambulatory legs with dactyls not shorter than propodi. Segments sparsely hairy with short, fine setae. Very distinctive pigment pattern as given below.

Anterior carapace slightly longer than broad, surface pitted, hairy on lateral margins. Front between lateral projections very straight except for small, broadly triangular rostrum which is in advance of front.

Eyestalks as long as, or longer than, front. Ophthalmic acicles acute, closely approximated, armed with 2-4 spines, terminal being largest.

Antennular peduncles do not extend beyond cornea.

Antennal peduncles reach from two-thirds to three-quarters length of eyestalks. Antennae extend to tips of legs. Acicles armed with 3-5 spines on inner margin in addition to terminus, usually one on outer margin.

Color. Olive green stripes on cream to light brown background. Stripes often fade to dark gray on orange background after formalin and/or alcohol. Chelipeds, until preserved a considerable time, light with darker, olive spines, rather than dark with light spines as in the two preceding species. Diagnostic color pattern of legs as follows: Dactyl with total of 4 dark stripes (one on superior margin, one on inferior, one on each side) separated by lighter stripes of approximately the same width; propodus similar; merus with an extra light and an extra dark stripe on each side, the stripes on the medial side being somewhat diffuse; carpus with 2 dark, 3 light stripes distinct on lateral side, but medial side indistinctly pigmented.

Size. L.c. male, 13 mm; female, 14 mm.

Range. Florida, from Miami southward; West Indies to South America, according to others.

Type locality. Cuba.

Type. Not traced.

Discussion. As may be seen from the synonomy, there has been some question as to the proper name for this species. Although Herbst did not give a locality for his type of *sclopetarius,* he described three other West Indian hermit crabs in the same work and his description and illustration are consistent with specimens from this area. However, Yap-Chiongco (1938) found a Pacific species which he assigned somewhat doubtfully to *C. sclopetarius.* A comparison of Philippine and West Indian material has not been possible to date and until such a comparison is made there will be a question whether Herbst's description is applicable to more than one species. Unfortunately, the matter may never be settled with certainty unless other information is brought to light, for according to Dr. H. E. Gruner (personal com-

munication) Herbst's type is no longer in the collections at Berlin where some of his material is still kept, and presumably it has become lost during the course of time. In view of the above, it would seem advisable to retain Saussure's name *cubensis* for this species.

Remarks. This is the least common of the four species of *Clibanarius* in the south Florida area. It apparently prefers a rock and sand bottom.

Material. 1 non-ovig. female and 1 male; north Key Largo, 12 May 1957, Provenzano.

1 non-ovig. female and 11 males; 12 mi. S. of Greyhound Key, 12 Oct. 1957, R. Manning.

1 male; Matheson Hammock, just S. of Miami, 27 Jan. 1958, R. Manning. UMML 32: 1087.

1 non-ovig. female; Boca Raton, about 40 mi. N. of Miami, 15 March 1958, William Rosselit.

Clibanarius vittatus (Bosc, 1802)
Fig. 5D

Pagurus vittatus Bosc, 1802: 78, pl. 12, fig. 1.
Clibanarius vittatus, Stimpson, 1862: 83; Hay and Shore, 1918: 410.

Diagnosis. Dactyls of ambulatory legs distinctly longer than propodi. Laterally, two median longitudinal fine white stripes separated by broad dark stripes; on dactyl and propodus a similar thin white stripe partially visible laterally along upper margin, and another along lower margin.

Description. Chelipeds equal, sparsely hairy, covered with short spines, each pigmented darker than basic color of hands. Dactyls more than half length of hands, which are 2 times longer than broad. Hands reach to base of ambulatory dactyls. Spines of hands somewhat blunt, in contrast to conspicuous spine on median antero-dorsal margin of carpus. One or more spines on antero-lateral margin of merus.

Ambulatory legs with dactyls longer than propodi. Conspicuous spine at antero-dorsal margin of carpus of both pairs, with sometimes an accessory spine on first pair. Dactyls with row of very small but sharp spines along inferior margin. Color patterns as below.

Anterior carapace slightly longer than broad, smooth, with inconspicuous punctae. A few fine hairs along lateral margins. Rostrum very small, broadly triangular, slightly in advance of front.

Eyestalks usually equal in length, but right may be slightly shorter than left occasionally. Eyestalks about as long as width of anterior carapace. Ophthalmic acicles very narrow, approaching each other at the tips, but well separated at bases, with 1-4 spines of which terminal is largest.

Antennular peduncles reach ends of eyestalks.

Antennal peduncles reach at least three-fourths length of eyestalks. Acicles with 3-5 terminal spines. Antennae reach tips of ambulatory legs.

Color. In life, greenish to dark brown, with gray to white stripes. Antennular peduncles light above, dark laterally, with orange flagella. Propodus of each ambulatory leg with 4 pairs of light stripes around segment, running longitudinally, continuous with similar stripes on

dactyl and carpus. One of the ventrally placed stripes usually somewhat diffuse.

Size. L.c. male, 23 mm; female, 22 mm.

Range. From North Carolina southward at least as far as the upper Florida Keys; west coast of Florida, including Alligator Harbor (Wass, 1955), also at mouth of Rio Grande (Stimpson, 1862). Alcock (1905: 160) gave Brazil as a reported locality also, presumably on authority of Moreira (1901).

Type locality. On the coasts of Carolina?

Type. Not traced.

Discussion. Hay and Shore (1918) gave measurements of a female somewhat larger than any of the material examined in this study. Very young specimens may have the lateral pair of prododal white stripes fused, giving the appearance of a single medial light stripe similar to *C. cubensis,* but other features such as the longer dactyls in *C. vittatus* will separate these young specimens.

Remarks. In south Florida waters this species seems to be taken most frequently in *Nerita* and *Fasciolaria* shells.

Material. 7 young females and 18 young males; 12 mi. S. of Greyhound Key, 12 Oct. 1957, R. Manning.

1 ovig. female; Virginia Key flats west of Seaquarium, 28 Oct. 1957, R. Manning.

2 non-ovig. females and 1 male; Matheson Hammock, just S. of Miami, 27 Jan. 1958, Manning and Provenzano. UMML 32: 1081.

2 non-ovig. females and 1 male; Crawl Key, 28 Jan. 1958, H. Kumpf.

2 non-ovig. females; north Key Largo, 8 March 1958, J. McMahon.

Genus *Dardanus* Paulson, 1875

Pagurus Fabricius, 1798: 410 (in part). Dana, 1851: 449. Brandt, 1851 (*non Pagurus,* Latreille, 1810). Stimpson, 1859: 223. Alcock, 1905: 78.
Dardanus Paulson, 1875: 90.
Pagurias Benedict, 1901: 141.
Dardanus, Rathbun, 1902: 33.

Chelipeds usually unequal and dissimilar, left much the larger. Finger tips corneous, and somewhat spooned, especially those of minor cheliped. Fingers move in obliquely vertical plane.

Rostrum absent.

Fourth pereiopods subchelate; 5th pair chelate.

Eyestalks stout, ophthalmic somite exposed. Ophthalmic acicles large and widely separated.

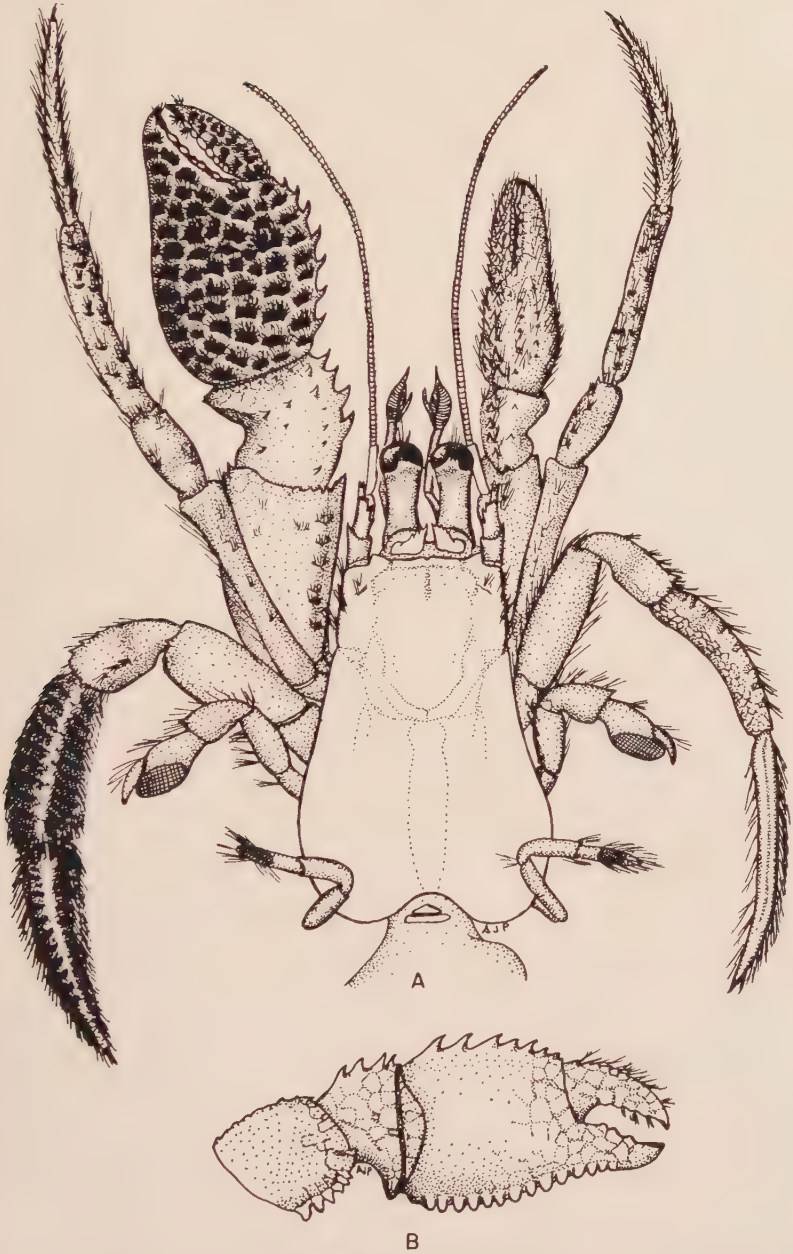

FIGURE 6. *Dardanus venosus* (H. Milne-Edwards, 1848), x 2. A. Anterior body. Note ridge on second left ambulatory leg. B. Inner surface of major manus showing some of the "veins" which give the species its name.

Antennae long and non-setose.

Exopods of all three pairs of maxillipeds with well developed flagellum; endopod of first maxillae non-flagellate.

Dardanus venosus (H. Milne-Edwards, 1848)

Fig. 6

Pagurus venosus H. Milne-Edwards, 1848: 61.
Pagurias insignis, Benedict, 1901: 141.
Dardanus venosus, Verrill, 1908: 441-447, figs. 58, 59; Rathbun, 1920: 329; Schmitt, 1935: 201, fig. 62.

Diagnosis. Second left ambulatory leg with longitudinal ridge, crossed with rugae. Fingers and legs covered with network of fine red lines. Antennal peduncles do not exceed eyestalks in length.

Description. Chelipeds unequal, left much larger than right. Finger tips black, corneous, spooned. Outer surface of major manus covered by scale-like tubercles separated by fan-shaped fringes of appressed hairs. Inner surface smooth. Seven sharp horny-tipped spines projecting forward along upper margin of major manus. Continued as row of smaller spines on movable dactyl, and as well developed spines on carpus. Carpus with smaller but sharp spines scattered over surface. Right chela narrower, lacking scale-like tubercles on lateral surface. Long setae rather than appressed bristles.

Ambulatory legs with dactyls longer than propodi, those of first pair longer than dactyls of second pair. Dactyls with many coarse light-colored setae, other segments with fewer, along upper and lower margins. Second left ambulatory leg markedly different from all others. Dactyl and propodus broadened, fringed with hairs, and with longitudinal ridge laterally, accented by slight groove parallel to it. Ridge crossed with numerous rugae similar to scale-like tubercles of major manus.

Anterior carapace slightly longer than width of front. Smooth, with few hairs and some deep lines near sides. Rostrum wanting, lateral projections forming sharp angles at antero-lateral corners of carapace.

Eyestalks stout, slightly constricted in middle, length measured from front scarcely more than three-fourths width of front. Eyestalks extend to tips of antennal peduncles or slightly beyond. Tuft of setae just back of cornea. Ophthalmic acicles widely separated, with straight inner margins, blunt tips carrying several spines.

Antennular peduncles exceed cornea by one third of last peduncular segment.

Antennal peduncles reach to tips of eyes. Acicles short, reaching but halfway up eyestalks, armed with small but sharp spines.

Color. Ambulatory legs banded transversely with broad red bands. Legs and inside surfaces of chelipeds, also fingers of hands, reticulated with fine red lines which give the species its name. Scale-like tubercles of manus and rugae of second left leg are blue to purple. Ophthalmic acicles may be white.

Size. L.c. male, 17 mm; female, 23 mm.

Range. Bermuda, southern Florida, West Indies to Brazil.

Type locality. Guadeloupe.

Type. Not traced.

Discussion. Verrill gives a very detailed description of this species and compares it with its close relative *D. insignis* (Saussure, 1858). The latter species lacks the longitudinal ridge on the propodus of the second left ambulatory leg, and has the eyestalks much shorter than in *D. venosus,* among other things.

Remarks. The species is fairly common in the Biscayne Bay area, many young having been taken from the sand and grass flats beside the Marine Laboratory at Bear Cut in the spring of 1958. Schmitt says it is found to a depth of 50 fathoms.

Material. 1 male; Bear Cut, Biscayne Bay, 9 Feb. 1958, Provenzano.
1 male; S. end of Bahia Honda Bridge, ocean side, 9 March 1958, Provenzano. UMML 32: 322.
1 specimen; Tortugas shrimp grounds, 10-18 fathoms, 10 March 1958, R. Manning. USNM 101263.
1 non-ovig. female; Ragged Key, 30 March 1957, Provenzano.
1 non-ovig. female; Bache Shoals, 3 May 1957, Gene Cope.
1 non-ovig. female and 1 male; Cape Fla. flats, Biscayne Bay, 13 July 1948, H. Doochin.

Genus *Isocheles* Stimpson, 1859

Isocheles Stimpson, 1859: 235. Alcock, 1905: 162.

Chelipeds similar, equal or subequal, left may be slightly larger; fingers move horizontally; finger tips corneous, acuminate.

Fourth pair of pereiopods subchelate, 5th pair chelate.

Rostrum obsolete, not in advance of front.

Eyestalks long and slender; ophthalmic acicles approximated, armed with very small, blunt tubercles along lateral margin.

Antennae short, very hairy.

Alcock (1905) states that this genus appears to differ from *Clibanarius* only in having the antennal flagella very short and setose, and the fingers of the chelipeds acuminate. He further says that *Holopagurus* Holmes, 1900 seems to differ from *Isocheles* only in having the left cheliped larger than the right. As will be pointed out below, this character may not be reliable in distinguishing these nominal genera and there is every indication that *Holopagurus* and *Isocheles* are synonymous.

Isocheles wurdemanni Stimpson, 1862

Fig. 7

Isocheles wurdemanni Stimpson, 1862: 85.

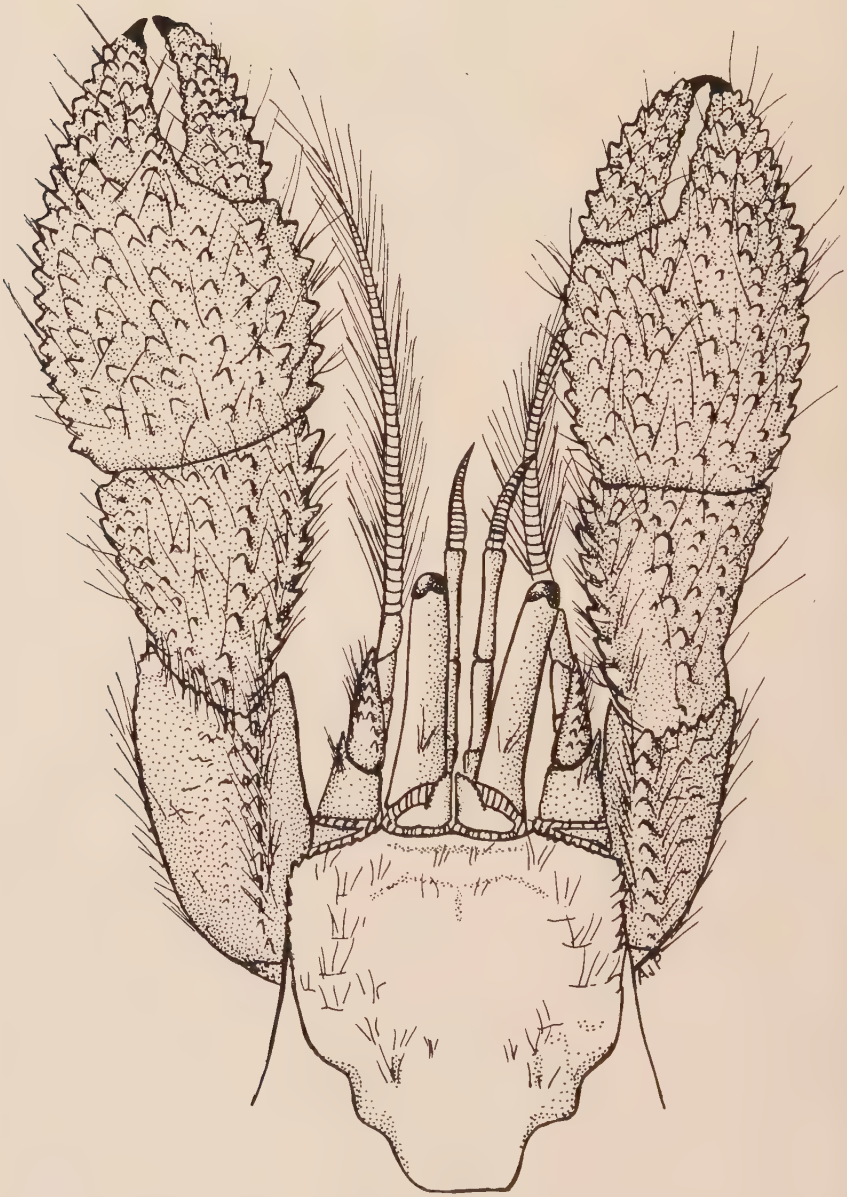

FIGURE 7. *Isocheles wurdemanni* Stimpson, 1862, x 6.

Diagnosis. Chelipeds subequal, left may be larger than right. Hands covered with blunt tubercles; finger tips corneous, but acuminate. Antennae short and very setose.

Description. Chelipeds subequal, left slightly larger than right. Upper surface of hands covered with blunt, medium tubercles arranged in ill-defined rows. Fingers corneous, but acuminate rather than spooned. Chelipeds with long fine hairs, which are also plentiful on other parts of the body. Left chela reaches just to base of first ambulatory dactyl. Carpus with two rather strong longitudinal rows of non-corneous spines on upper surface, separated by a smooth groove. Smaller spines scattered over rest of surface of carpus. Merus smooth on inside, granulated on outside surfaces, created dorsally with a row of sharp spines.

Ambulatory legs granulated, very sparsely setose, dactyls longer than propodi.

Carapace with marked double-lobed post-frontal groove. Anterior portion as long as broad, lateral margins spinous, hairy. Rostrum obsolete, exceeded by lateral projections of front.

Eyestalks slender, nearly straight, exceeding antennal peduncles by length of cornea. Ophthalmic acicles approximated, with minute tubercles on lateral margins.

Antennular peduncles equal to or slightly exceeding eyestalks in length.

Antennal peduncles fall short of equaling eyestalks. Acicles reach about three-fourths length of eyestalks, and are armed with small spines on inner and outer margins.

Color. Stimpson mentioned reddish vittae, or stripes, on the upper surface of the eyestalks. Wass (1955) says the species is white.

Size. L.c male, 15 mm; female (ovig.), 9 mm. Stimpson gave measurements of a somewhat larger specimen.

Range. Texas, west coast of Florida, and (according to specimen records at USNM) Louisiana and Venezuela.

Type locality. Gulf of Mexico, at mouth of Rio Grande.

Type. Not traced.

Discussion. The above description and the illustration were based on 5 specimens from Texas. All, including the large male on which the illustration is based, have the left hand slightly larger than the right. This is also true of the *Silver Bay* specimen. However, the Gulf Beach specimen was found to have the hands equal in size. Thus variation in the character within the species throws the status of *Holopagurus pilosus* Holmes, 1900, described from California, into doubt. That species has a great resemblance to an overgrown *Isocheles wurdemanni,* but a critical study of the relationships of these and other species of *Isocheles* is needed.

Remarks. The specimen mentioned by Wass (1955: 151) and reexamined in this study was taken in an *Oliva* shell as was the *Silver Bay* specimen, but the Texas material all came out of drill shells (*Thais*).

Material. 1 male; Gulf Beach across Alligator Point from Fla. State University Marine Lab., 16 Sept. 1952, Marvin Wass. USNM 95593.

1 ovig. female and 4 males; 400 yards off Galveston Beach, Texas, 1953, Don Moore. UMML 32: 1095.

1 juv. male; *Silver Bay* stat. 557-558, cruise 10 (27°44′N, 82°46-47′W) 20 ft., 23 July 1958.

Genus *Petrochirus* Stimpson, 1859

Petrochirus Stimpson, 1859: 233.

Chelipeds subequal, but right slightly larger than left. Fingers of right hand with coarse tubercles on opposing edges, tips calcareous. Fingers of left hand with sharp opposing, cutting edges, extreme tips black, corneous. Fingers move obliquely.

Rostral projection rounded, on a line with similarly shaped lateral projections.

Fourth pereiopods subchelate; 5th pair chelate.

Eyestalks slender; ophthalmic acicles well developed, separated.

Antennae long and non-setose.

Exopods of all three pairs of maxillipeds with flagellum.

Petrochirus bahamensis (Herbst, 1796)

Fig. 8

Cancer bahamensis Herbst, 1796: 30.

Petrochirus granulatus, Stimpson, 1859: 234.

Petrochirus bahamensis, Benedict, 1901: 140; Hay and Shore, 1918: 410; Schmitt, 1935: 206. fig. 66.

Diagnosis. Larger right hand with calcareous finger tips. Both chelae covered on upper surface with granules in groups separated by semicircular fringes of appressed hairs. Antennal peduncle with longitudinal red stripe on each side and one ventrally; antennal flagellum with wide alternating transverse bands of red and white.

Description. Chelipeds unequal, right slightly larger. Fingers of right hand tuberculate on opposing surfaces, calcareous tips; those of left hand spooned, with cutting edges and black, horny extreme tips. Both chelae with irregularly placed groups of granules or low tubercles, separated from other groups by appressed hairs which are dark near bases, but light on tips. Under sides of chelae granulated. Longitudinal groove from base of movable dactyl to carpal joint is lateral to inner margin or crest of hand. Carpus with 5 well developed, black tipped spines along inner margin. Groups of separate granules have become, on the upper surface of carpus, smooth white scale-like structures with small sharp spines at anterior edges. Inner surface of merus divided into two red areas by broad diagonal stripe, almost white.

Ambulatory legs with very dense rows of setae on dactyls, more clusters of hairs on under sides of propodi. Dactyls slightly twisted. Propodi and carpal segments, especially of first pair of legs, with dorsal row of black tipped spines. Dactyls longer than propodi.

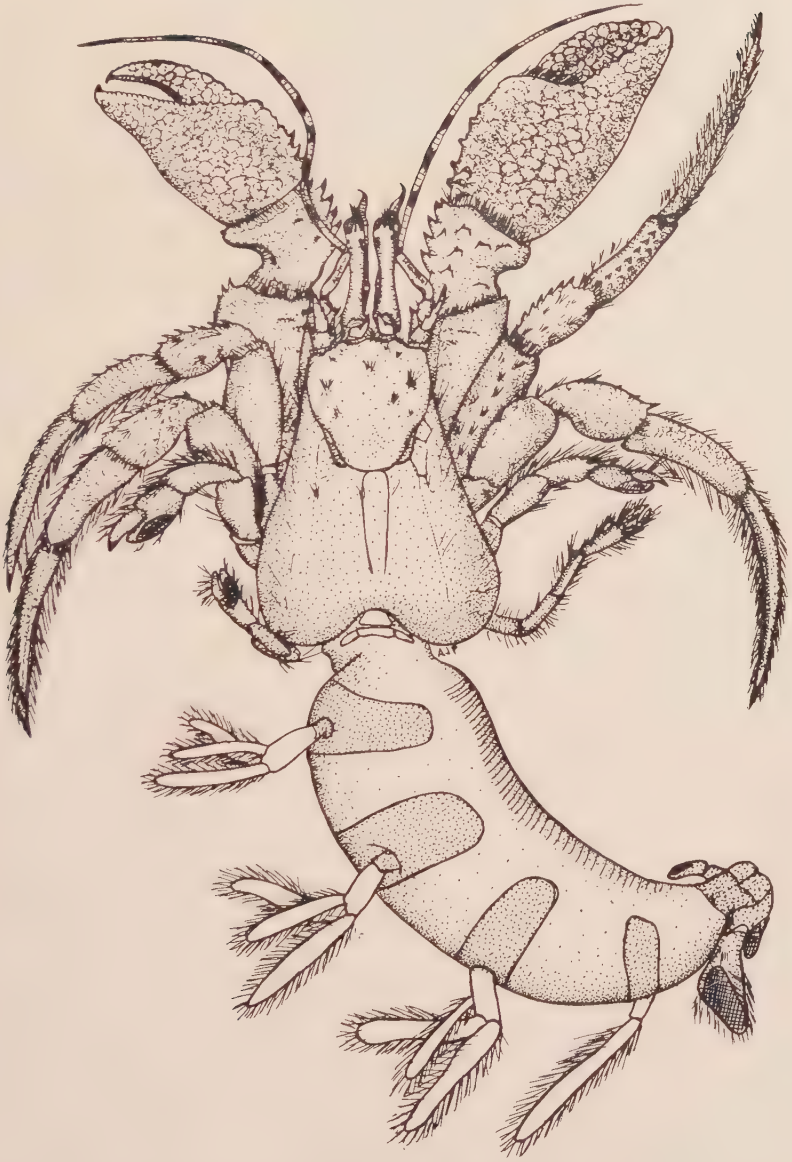

FIGURE 8. *Petrochirus bahamensis* (Herbst, 1796), x ½. A female specimen, with well developed triramous pleopods.

Anterior carapace as broad as long, rostral and lateral projections of front rounded, about equal in prominence, all in advance of antero-lateral corners of carapace. Latter with tufts of hairs prominent along sides.

Eyestalks straight rather than noticeably curving, a tuft of setae just posterior to cornea, lighter tuft near base of eyestalk. Ophthalmic acicles broad basally, but very acute anteriorly with indistinct serrations.

Antennular peduncles reach end of eyestalks, persistent pigment patterns as indicated below. Somewhat flattened laterally.

Antennal peduncles fall short of cornea. Acicles hairy, with minute but sharp spinules. Antennae may reach beyond chelipeds, especially in young specimens.

Color. Generally reddish, the transverse banding of red and white on the antennae is very striking. The antennal and antennular peduncles are longitudinally striped with red and white. The chelipeds are reddish except for between the dactyls and for the smooth white spots on the carpal segments.

Size. L. c. male, 75 mm; female, 37 mm.

Range. North Carolina to Brazil, including northwestern Florida.

Type locality. Bahamas.

Type. No longer with Herbst's collection at Berlin, and believed destroyed.

Discussion. Benedict, Hay and Shore, Alcock, and other authors indicate in synonymies that *Petrochirus granulatus* (Olivier, 1811) is the same species, and if so, then the range is considerably expanded, reaching at least to the Cape of Good Hope. I have not examined specimens from outside the West Indian region and have no statement to make on this matter at this time.

Remarks. This species attains by far the largest size of any West Indian hermit known and this feature alone makes it conspicuous in shallow waters. The larger specimens are usually taken in *Strombus gigas,* often with a commensal porcellanid crab, *Porcellana sayana.* Specimens have been dredged from as deep as 18 fathoms on the Tortugas shrimping grounds.

Material. 1 young female; Bear Cut, Biscayne Bay, Feb. 1957, student field class.

2 specimens; Tortugas shrimp grounds, Fla. from 10-18 fathoms, 10-12 March 1958, R. Manning. USNM 101262.

1 young female and 1 young male; Bear Cut, in front of Marine Lab, 9 Feb. 1958, Provenzano.

1 male; S. end of Bahia Honda Bridge, Fla. Keys, 9 March 1958, Provenzano. UMML 32: 1076.

1 non-ovig. female; outside reef off Marathon, Fla., 5 May 1958, Gene Shinn. UMML 32: 1077.

2 males; Key West, 21 March 1958, C. R. Robins & W. R. Courtenay, Jr. UMML 32: 1089.

Genus *Paguristes* Dana, 1851

Paguristes Dana, 1851: 269. Alcock, 1905: 30.

Chelipeds similar, equal or subequal, or one (usually the left) may be larger. Fingers move horizontally, tips usually corneous, may be calcareous.

Fourth pair of pereiopods not cheliform, dactyl being terminal, 5th pair cheliform.

Rostrum usually well developed.

Eyestalks long and usually slender. Ophthalmic acicles well formed, usually spiniform and widely separated.

Antennal acicle well formed. Antennal flagellum moderate or short in length, often setose.

Exopods of all three pairs of maxillipeds with well developed flagellum; endopod of first maxilla has a recurved flagellum.

In males, first two abdominal somites each carry a pair of uniramous appendages modified for sexual purposes. In females, the first abdominal somite alone carries a pair of uniramous appendages. From left side of fourth somite in females, a fleshy foliaceous lobe protrudes, overlapping the preceding three pleopods and forming a brood pouch, except in *P. anomalus*.

A Key to the Littoral Florida Species of *Paguristes*

1. Fingertips of chelipeds spooned. Rostrum a well developed, acute projection 2
   Fingertips of chelipeds acuminate. Rostrum obsolete, broadly rounded .... *hummi*
2. Hard parts rich red or rust-brown, heavily spotted with white. Setae simple, unbranched. 3
   Hard parts not red spotted with white. Setae with numerous very fine side branches 4
3. Hairs on hands long, conspicuous, obscuring spines ..... *puncticeps*
   Hairs inconspicuous, not obscuring spines ..... *grayi*
4. Eyestalks and antennules white with rings of black. Female with brood pouch ..... *tortugae*
   Eyestalks and antennules not ringed with black. Female without brood pouch ..... *anomalus*

Paguristes hummi Wass, 1955

Fig. 9

Paguristes hummi Wass, 1955: 148, figs. 1, 2, 3, 4.

Diagnosis. Fingertips of both chelipeds corneous, but acuminate, rather than spooned. Rostrum obsolete, broadly rounded. Antennular peduncles reach past cornea by half the length of last segment. Antennae very hairy.

Description. (Note:—The recent description of this species is quite detailed.

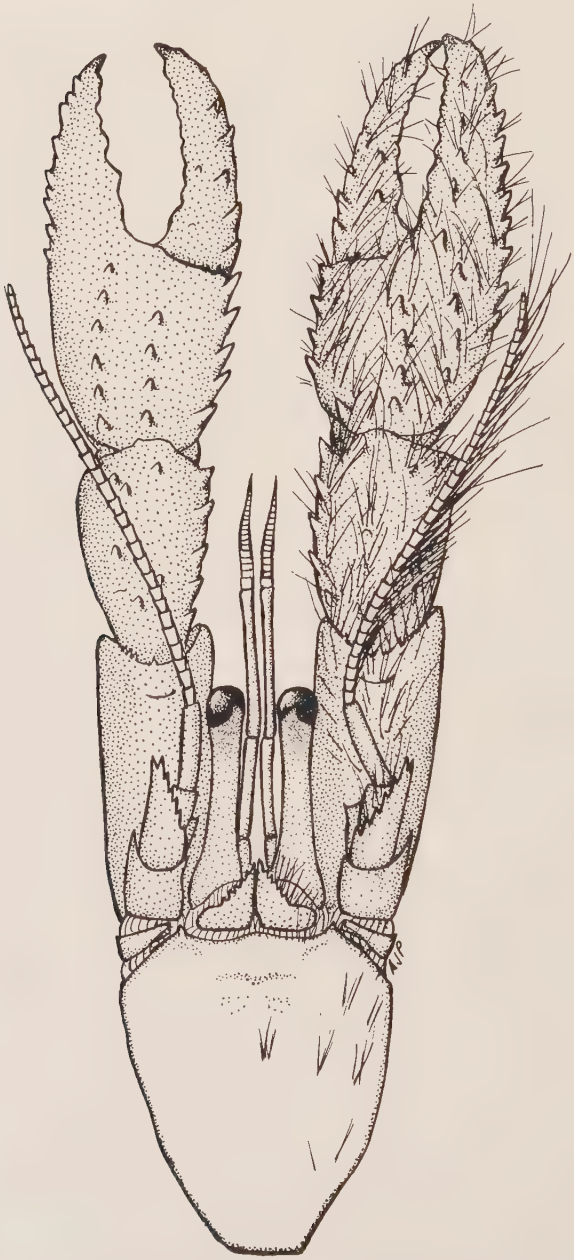

FIGURE 9. *Paguristes hummi* Wass, 1955, x 10. Hairs have been removed from the left side to show spination.

The following is a modification based on additional material.)

Chelipeds with fingertips acuminate rather than spooned. Hands equal and similar. Manus with 4 distinct rows of spines on upper surface, 6 spines in inner row, 4 in second, 5 in third, and about 15 in outer row. Long setae usually rising from bases of spines. Carpus with about 6 spines on inner margin, an even row of about 9 irregularly sized spines on outer margin.

Ambulatory legs slender, dactyls much longer than propodi. First pair with small spines along upper edge of merus and propodus, second pair with tubercles only. Both pairs moderately setose.

Anterior portion of carapace longer than wide. Deep transverse depression posterior to front. Rostrum obsolete, shorter than lateral projections, not reaching bases of ophthalmic acicles.

Eyestalks measured from front as long as width of latter. Slightly exceeding antennal peduncles. Eye pigment shows through exoskeleton posterior to cornea. Ophthalmic acicles

> medially adjacent from base to apex except for shallow indentations near the bases; base subquadrate, lateral projections produced antero-laterally; apical regions armed with 4-7 spines anteriorly, the largest at the tip.—Wass.

Antennular peduncles exceeding cornea by at least half length of last (third) segment when peduncles are fully extended.

Antennal peduncles fall short of tip of cornea. Acicles stout, reaching to last quarter of eyestalks, 5-6 spines on inner margin in addition to single or double terminal spine. No spines on outer margin.

Color.

> In life the outstanding color mark is an iridescent blue patch on the inner surface of the merus of the cheliped; this area is bordered anteriorly by a narrow black line, followed by a similar yellow line. In alcohol the blue and yellow fade and the black line becomes brick red; the ambulatory legs have pinkish bands and the chelae are marked with blotches of similar coloring.—Wass.

Size. L.c. male, 7 mm; female (ovig.), 3 mm.

Range. West coast of Florida, including Alligator Harbor, Clearwater Beach, Muilet Key in Tampa Bay, and Marco Island.

Type locality. Alligator Harbor, Franklin County, Florida.

Type. Deposited in USNM. In addition to the holotype (Cat. No. 95596), Wass gives data on 59 specimens deposited as paratypes in USNM.

Discussion. This species, of the 5 *Paguristes* in Florida shallow waters, is the only one with acuminate fingertips, the others all having rather distinctly spooned dactyls on the chelipeds. It also has very long hairs on the antennae, and in these two respects bears some resemblance to *Isocheles wurdemanni,* but the large number of dissimilar features of these species will allow ready separation. Wass discusses the relationship of this species with others of the genus.

Remarks. None.

Material. 11 males and 1 ovig. female; washed ashore at Marco Beach, 3 Feb. 1957, R. Manning. UMML 32: 1083.

2 males; on sand around pilings at Clearwater Beach, 17 May 1958, Provenzano.

Paguristes puncticeps Benedict, 1901

Fig. 10A

Paguristes puncticeps Benedict, 1901: 144, pl. 4, fig. 5; pl. 5, fig. 2.

Diagnosis. Hard parts with innumerable small white spots on reddish background. Long unbranched hairs obscuring spination of upper surface of hands and first ambulatory propodi. Inner margin of manus almost a straight line, very little indentation at base of dactyl.

Description. Chelipeds somewhat pointed, inside margin of manus almost a straight line. Fingers flattened, spooned, with a white tooth on inside of each at tip. Hands covered with sharp, corneous-tipped spines, obscured by long hairs on most of upper surface of hand. Carpus with 3-4 large black-tipped spines on inner margin. Long hairs obscure upper surface which has small, inconspicuous, corneous-tipped spines. Dorsal longitudinal groove on carpus, when present, indistinct.

Ambulatory legs hairy on upper and lower margins, especially of first pair. Propodus and dactyl of first pair with row of well developed forward-pointing black-tipped spines on upper edge, obscured by hairs. Dactyls distinctly longer than propodi.

Anterior carapace slightly longer than wide, rostrum extending well beyond front, but base posterior to tips of lateral projections. Lateral spines before and behind cervical groove not prominent.

Eyestalks straight, equal to front when measured therefrom. Ophthalmic acicles separated by rostrum and with simple, slender, acuminate anterior lobe armed with terminal spine.

Antennular peduncles do not reach cornea.

Antennal peduncles reach just beyond middle of eyestalks. Acicles with 1-2 spines on inner edge, 2-3 on outer edge in addition to terminus, all obscured by long hairs. Antennae reach ends of chelipeds, but not ends of ambulatory legs, and have few, short, inconspicuous hairs.

Color. One specimen in life was rust-brown, covered with white spots, the cornea of the eye being blue. Red color and white spots ringed with dark red retained for a time in alcohol, but much longer in formalin. See Discussion.

Size. L.c. male, 13 mm; female, 12 mm. (The above measurements were taken from Miami material.) The largest type male is 17 mm and there is in the USNM a Cuban ovigerous specimen with a L.c. of 20 mm.

Range. Wass (personal communication) has found it along northwestern Florida. It is not uncommon in south Florida from Miami southward, and probably occurs generally in the West Indies.

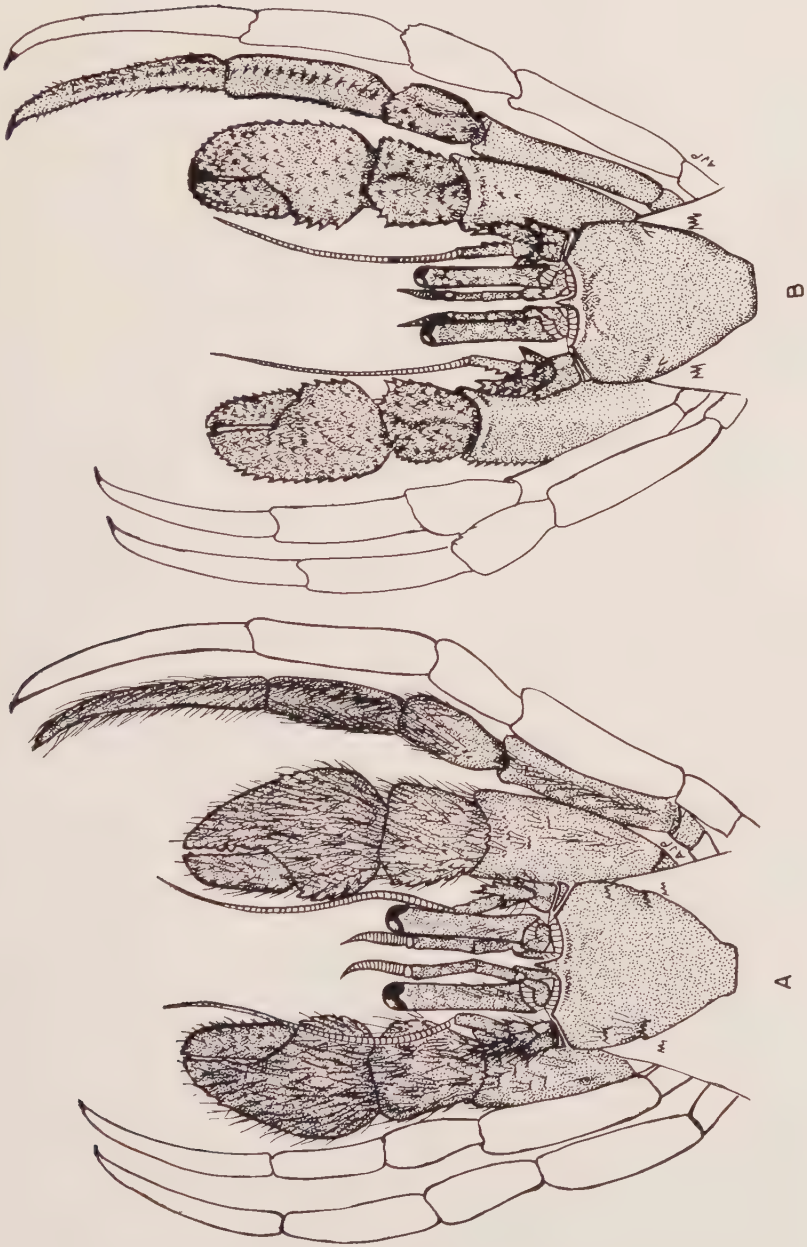

FIGURE 10. A. *Paguristes puncticeps* Benedict, 1901, x 3. B. *Paguristes grayi* Benedict, 1901, x 1.5.

Type Locality. Jamaica.

Type. Type material in the USNM (Cat. No. 29203) consists of 9 males and one specimen of undetermined sex, all damaged considerably.

Discussion. This species is very close to *P. grayi,* one of the most striking similarities being the color pattern. However, it has many features in common with *P. sericeus* and *P. rectifrons* also. I have not examined critically the former, but below are listed specimens of *P. rectifrons* which were compared to specimens of *P. puncticeps* during this study. Although the color patterns and other features of these species are similar, two features which seem to set them apart are: that in *rectifrons* the antero-lateral angles of the carapace approximate right angles, whereas in *puncticeps* the front slopes back to the sides much less acutely; further, in none of the *puncticeps* fresh enough to retain color did the eyestalks fail to bear numerous white spots like the rest of the hard parts, but in the few specimens of *rectifrons* examined (all still with pigment) the eyestalks were unspotted, solid orange-red.

Material. P. puncticeps: 1 male; Tortugas shrimp grounds (10 fath.), 10-12 Mar. 1958. Manning. UMML 32: 1094.

9 males and one specimen of undetermined sex, syntypes; Jamaica, 1-11 March 1884, *Albatross.* USNM 29203.

1 ovig. female; Cardenas Bay, S. shore Hicaces Pen. off 61st St., Varadero, Mantanzas Prov., Cuba, 24 Jan. 1957, Waldo L. Schmitt. USNM 99921.

1 non-ovig. female; Punta Colorado, Cuba. USNM 48648.

2 males; Biscayne Bay ; 1937, J. F. W. Pearse. MCZ 9820.

1 non-ovig. female; rocks, E. end of MacArthur Causeway, Biscayne Bay, 8 March 1958, Robert Work. UMML 32: 1090.

1 male; Bear Cut, Biscayne Bay, 8 Oct. 1957, student field class. UMML 32: 1091.

1 non-ovig. female; Soldier Key, 27 June 1936. UMML 32: 92.

1 male; near *Porites* bed, N. side of Indian Key, 1 Feb. 1958, Provenzano. UMML 32: 1092.

P. rectifrons: (all with unspotted eyestalks) 1 ovig. female and 1 male; Tortugas shrimp grounds (9-15 fath.), 10-12 March 1958, R. Manning. To be deposited in UMML.

1 male; Heald Bank (Sabine), Texas; W. G. Hewatt 54871 from Magnolia Field Res. Lab. USNM 97657.

1 male; 29°21-22′N, 84°41′W, 15 fathoms, 25-26 July 1958, *Silver Bay* stations 585-586. Retained by author.

1 ovig. female, 1 non-ovig. female, 1 male, and 1 specimen of undetermined sex; 27°44′N, 82°46-47′W, 23 July 1958, *Silver Bay* stations 557-558. To be deposited in USNM

Paguristes grayi Benedict, 1901

Fig. 10B

Paguristes grayi Benedict, 1901: 146, pl. 5, figs. 1 and 1a; Schmitt, 1935: 202, fig. 63.

Diagnosis. Hard parts with innumerable small white spots on red background. Spination of upper surface of hands and first ambulatory propodi not obscured by long hairs, only short unbranched bristles present. Inner margin of manus not a straight line, but with prominent indentation at base of dactyl.

Description. Chelipeds rounded at tips in dorsal profile, as opposed to pointed. Inside margin of palm extends beyond line of margin of movable dactyl so that there is a break in the inner margin of hands. Fingers corneous, spooned, not flattened at tips. Inside surface of each dactyl bears a single white tooth of varying size. Hands covered with white, black-tipped spines among which are scattered short bristles, not longer than spines. Carpus with forwardly directed spines on upper surface, largest on antero-medial margin. Spineless dorsal longitudinal groove usually well marked.

Ambulatory legs with dactyls distinctly longer than propodi. Row of very well developed sharp, black-tipped forward pointing spines on upper edge of propodus and dactyl of first pair, not obscured by short bristles. Smaller spines on medial surface of propodus.

Anterior carapace slightly longer than wide. Rostrum extending well beyond lateral projections, but base of rostrum lies posterior to tips of lateral projections. White lateral spines before and after groove separating anterior and posterior carapace well developed.

Eyestalks straight; even when measured from lateral projections, hardly as long as greatest width of anterior carapace. Acicles with simple, somewhat truncate anterior lobe armed with a very well developed terminal spine.

Antennular peduncles do not reach cornea.

Antennal peduncles reach more than half way up length of eyestalks. Acicles with 2-3 spines on inner margin, 3-4 on outer margin in addition to terminus. Antennae reach just beyond tips of chelipeds, have few short inconspicuous hairs.

Color. In life, maroon or deep red, with innumerable white spots all over hard parts, as in previous species. Color patterns persistent in alcohol and formalin.

Size. L.c. male, 24 mm; female, 21 mm.

Range. Florida Keys, Tortugas, Puerto Rico. Santo Domingo and probably generally throughout the West Indian region.

Type locality. San Antonio Bridge, San Juan, Puerto Rico.

Type. A female (L.c. 21 mm) in USNM (Cat. No. 42498). See Discussion.

Discussion. Upon inspection in June 1958 the jar containing the type was found to contain a total of three chelipeds, two of which apparently belong to the type, as they are *grayi* chelae, the other may be that of *P. puncticeps*. The species is quite closely related to *P. puncti-*

ceps and the similarity of color pattern may at first seem confusing but a little effort will reveal some of the many features in which the species differ.

Remarks. The species, while sometimes found with *P. puncticeps,* seems much less tolerant of soft bottom and poor circulation, apparently preferring rocky or reef bottom in waters of good circulation.

Material. Type: 1 female; San Antonio Bridge, San Juan, Puerto Rico. G. M. Gray. USNM 42498.

1 female; Tortugas, Fla.; 1928, A. S. Pearse. USNM 62180.

1 male and 3 non-ovig. females; S. end of Bahia Honda Bridge, Fla. Keys, 9 March 1958, Provenzano. UMML 32: 1093.

1 non-ovig. female; Puerto Sosua, Santo Domingo, July 1937, W. J. Clench. MCZ 9875.

1 non-ovig. female; Cape Santa Maria, N. end of Long Is., Bahamas, 10 July 1936, Harvard Bahama Expedition. MCZ 9442.

2 males; E. of Hen & Chicken Key, 5 June 1948, H. D. Doochin. UMML 32: 451.

1 non-ovig. female; Long Reef, Key Largo, Don Moore. UMML 32: 450.

1 non-ovig. female; Cat Cay, Bahamas, 4 May 1958, J. Randall.

1 non-ovig. female and 2 males; Indian Key, ocean side, 3 May 1958, Provenzano.

Paguristes tortugae Schmitt, 1933

Figs. 11 A, B; 12D

Paguristes tortugae Schmitt, 1933: 7, fig. 4; Schmitt, 1935: 204, fig. 64; Wass, 1955: 134, (in key, omitted by mistake in text).

Diagnosis. Fingertips of chelipeds corneous, spooned. Rostrum well developed, broadly triangular. Eyestalks and antennules white with black rings or bands. Dactyls of ambulatory legs scarcely longer than propodi. Setae bear side branches.

Description. (Note: The original description of this species is well detailed. The following modification is largely quoted from it.)

Chelipeds equal, tips of fingers corneous, spooned. Inside margins of movable dactyls, palms, and carpal segments straight so that the chelipeds fit closely together when retracted. This effect heightened by fringes of hairs along margins of hands, which give them squarish appearance. Hands as well as margins of ambulatory legs, extremely hairy, spination largely obscured.

> . . . the outer half of the palm and the outer margin of the fixed finger are beset with sharp, forwardly directed hooked spines, likewise the median area of the upper surface of the palm; inner margin of the hand similarly armed with three stout spines . . . The carpus of the right cheliped has five large spines on the inner margin, about as many slightly smaller spines on the outer margin, and three or four sharp spines on the anterior margin; the upper surface is more or less coarse-granulate with an approximately median row of sharp conical granules . . . The merus is armed with a sharp corneous-tipped spine near the anterior end of the upper margin and three

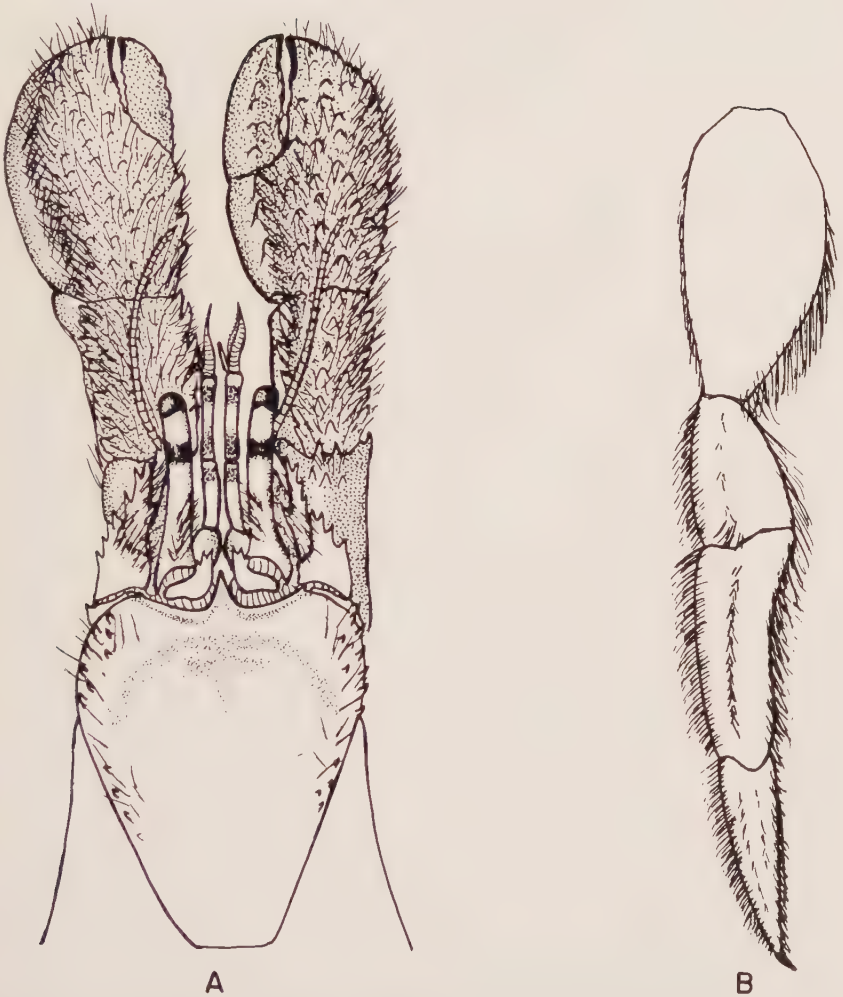

FIGURE 11. *Paguristes tortugae* Schmitt, 1933, x 8. A. Anterior body. B. Lateral view of second left ambulatory leg. See also Fig. 12D.

good, sharp, corneous-tipped spines on the anterior margin; otherwise general surface of joint is more or less scabrous, inner lower margin armed with three or four sharp spines.

Ambulatory legs with heavy fringes of hairs along upper and lower margins. The merus of the first right ambulatory leg is denticulated on the anterior margin; the carpus has a row of conical spines or tubercles on the upper margin and a somewhat irregular second row on the inner face, in line with a similar row of seven to nine spines on the inner face of the propodus, the

upper margin of which is armed with seven to eight conical, light corneous-tipped spines. About fifteen transverse tuberculiform ridges ornament the upper margin of the dactyl which terminates in a strong, dark blackish-brown claw. The opposite leg is similar but less prominently spined, while the second pair of ambulatory legs are quite without spines except two not very conspicuous ones among the hairy fringe, one at and the other close to the anterior end of the upper border of the carpus. The carpus is obscurely denticulate on the upper border, but this pair of legs, though somewhat scabrous, is quite smooth in comparison to the first pair.

Anterior carapace longer than broad. Rostrum broadly triangular, in advance of lateral projections of front.

Eyestalks straight, slender, as long as greatest width of anterior carapace. Ophthalmic acicles with 3-4 spines decreasing in size from the medial. Acicles separated by rostrum.

Antennular peduncles reach to base of cornea or slightly beyond.

Antennal peduncles reach three-fourths way up eyestalks. Antennae short, not reaching to ends of chelipeds, sparsely setose with very short hairs. Acicles obscured by hairs, armed with two spines on inner edge, at least three on outer edge in addition to prominent terminus.

Color. Usually whitish with the large spines on the inner margin of manus and carpus red. Occasionally hard parts are lightly tinted with green or purple. Most striking is the banding on the eyestalks and antennules, which consists, on the eyestalks, of a sometimes broken, single ring of black (on white), and on the antennules similar rings on the ends of the segments.

Size. L.c. male; 10 mm; female (ovig.) 7 mm.

Range. West coast of Florida, Florida Keys, (as far north as Miami), Dry Tortugas, and Puerto Rico. Probably in many other West Indian areas as well.

Type locality. Interstices of large *Porites* clumps off Fort Jefferson dock, Garden Key, Dry Tortugas, Fla.

Type. Ovigerous female, USNM Cat. No. 65840.

Discussion. There is some variability in color and in relative width of the rostrum. Schmitt discusses the relationship of this species to others of the genus, but he was unaware of the existence of *P. anomalus* Bouvier to which it has the closest resemblance of all. (See discussion under latter species.)

Remarks. This species prefers, but is not always found on, hard bottom. The specimens from Bahia Honda bridge were all taken in *Cerithium* shells, each between branches of the alcyonarian *Eunicea palmeri* Bayer. (Identification of latter by Dr. Frederick M. Bayer.)

Material. 1 male; Angel Fish Creek, north Key Largo, 17 May 1935. UMML 32: 109.

4 males; washed ashore at Marco Is., 3 Feb. 1957, R. Manning.

3 ovig. females and 3 males; south end of Bahia Honda bridge, Fla. Keys, 9 Feb. 1958, Provenzano. UMML 32: 1096.

1 non-ovig. female; Matheson Hammock, 27 Jan. 1958, Manning.

To be deposited in UMML:

2 males; Soldier Key, ocean side, 26 April 1957, C. R. Robins & W. R. Courtenay.

4 young females, one ovigerous; Government Cut, Miami, 20 April 1958, Provenzano.

1 ovig. female and 5 males; Government Cut, 5 May 1958, Provenzano.

1 male; Bear Cut, Biscayne Bay, 9 Feb. 1958, R. Manning.

1 male; Bear Cut, 5 March 1958, J. Klussmann.

2 ovig. females and 2 males; Long Key, 12 Oct. 1957, C. R. Robins & W. R Courtenay. (CRR-F-106).

1 non-ovig. female; Long Reef, 19 April 1958. G. Shinn.

Paguristes anomalus Bouvier, 1918

Fig. 12A, B, C

Paguristes anomalus Bouvier, 1918: 6, fig. 1.

Diagnosis. Finger tips spooned. Rostrum well developed, acute. Setae with numerous very fine side branches. Eyestalks and antennules without rings of black. Female without brood pouch.

Description. Chelipeds equal, finger tips black, corneous, spooned. Hands with low granules of varying size on upper surface, obscured by appressed hairs. Many hairs on upper surfaces of manus and carpus, forming well developed fringe along both margins. Fringe nearly conceals row of sharp corneous tipped spines along inner margin of hand and carpus. Merus with irregular row of denticles along inferior margin.

Ambulatory legs with dactyls not exceeding propodi in length. Row of corneous spines on inferior margin of propodus. Fringe of setae on upper and lower margins of dactyls and propodi. Propodi with 2 irregular series of striations along medial surface, bearing short hairs.

Anterior carapace much longer than broad. Rostrum well developed, acute, well in advance of lateral projections of front which are somewhat rounded.

Eyestalks shorter than front, slightly dilated at base, tapering to cornea. Ophthalmic acicles slender, armed with 2-4 sharp teeth.

Antennular peduncles do not exceed cornea.

Antennal peduncles reach to base of cornea. Antennae shorter than anterior carapace. Antennal acicles obscured by hairs, armed with 4-5 spines.

Color. Fresh specimens were pale green, the fingers of the hands being even lighter. No strongly marked pigment patterns were seen. Alcoholic specimens have blue antennae and there is some blue pigment on the eyestalks.

Size. L.c. male, 7 mm; female, 4 mm.

Range. Known only from the type locality and the Florida collections from Long Reef.

Type locality. Near San Diego de Cuba under old coral.

Type. On deposit at the National Museum in Paris.

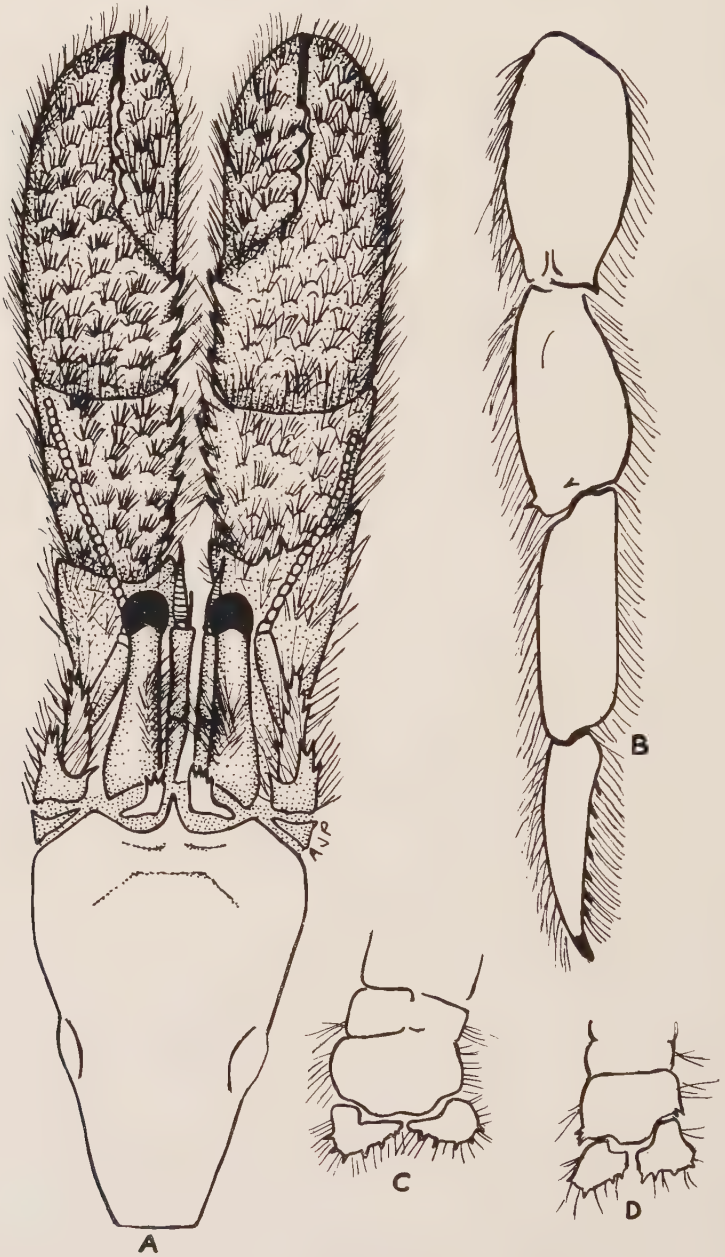

FIGURE 12. *Paguristes anomalus* Bouvier, 1918. A. Anterior body. B. lateral view of second left ambulatory leg. C. telson. D. *Paguristes tortugae*. Telson.

Discussion. This species is very similar in many respects to *P. tortugae* and alcoholic males may be difficult to distinguish from that species. One of the most striking similarities is in the fringes of branched hairs on chelipeds and legs. However, there are numerous details in which the species differ, the most important of course being the lack in the female of the brood pouch otherwise characteristic of the genus. Eyestalks are shorter than the front in *anomalus,* whereas those of *tortugae* are more nearly equal to the front. The pigment pattern of *tortugae* will immediately serve to distinguish it from *anomalus,* and there are differences in the telson armaments as well. The double row of striations on the inner surface of the propodus is found in both species and is not so easily used to separate the two.

Remarks. This species apparently is restricted to exposed waters rather than inshore shallows and further search along some of the reefs of the keys and in the West Indies may reveal a much wider distribution than is presently known.

Material. 1 ovig. female, 1 non-ovig. female, and 1 male; Long Reef, Fla. 19 April 1958, G. Shinn. UMML 32: 1134.

5 non-ovig. females and 6 males; Long Reef, 29 June 1958, G. L. Voss. At least 1 female and 1 male to be deposited in USNM.

Subfamily Pagurinae Latreille, 1802-03 (=Eupagurinae Ortmann, 1898)

This group is characterized by having the third maxillipeds well separated at the base by a sternum. Also, as Alcock noted:

> The right cheliped is usually vastly larger than the left, the left is never larger than the right; occasionally they are subequal.

Most of the genera are more characteristic of deeper waters, but the largest genus, *Pagurus,* is well represented in Florida shallows with at least 9 species.

Pagurus Fabricius, 1775

Pagurus Fabricius, 1775 (1798?): 411 (in part).
(Not seen). Type species, *Cancer bernhardus* Linnaeus.

Eupagurus Brandt, 1851: 105.

Bernhardus Dana, 1851: 440.

Eupagurus, Stimpson, 1858: 236; Milne-Edwards and Bouvier, 1893: 139; Alcock, 1905: 122; Bouvier, 1940: 129.

Chelipeds usually dissimilar and unequal, the right being much larger than the left. Very rarely subequal. Fingers move horizontally, tips calcareous, rarely corneous.

Fourth pereiopods subcheliform, 5th pair imperfectly chelate.

Rostrum either distinct or obsolete.

Eyestalks stout or slender. Acicles well separated.

Antennal acicles long, flagellum long, slightly or non-setose.

External (third) maxillipeds widely separated at bases by a sternum. Exopod of all three pairs of maxillipeds are flagellate. Endopod of first maxilla without a flagellum, but sometimes with a rudimentary one.

A Key to the Florida Littoral Species of *Pagurus*

1. Eyescales armed with 2 or more spines 2
   Eyescales unarmed or with single inferior spine 4
2. Rostrum acute ..... *pygmaeus*
   Rostrum obsolete 3
3. Stripes on legs extending entire length of each segment ..... *miamensis*
   Stripes on legs ending well before joints of segments ..... *brevidactylus*
4. Length of eyestalk at least 5 times greatest width 5
   Length of eyestalk not more than 3 and one-half times greatest width 6
5. Antennular peduncles do not extend beyond cornea; rostrum acute .. *marshi*
   Antennular peduncles extend beyond cornea; rostrum obsolete .. *annulipes*
6. Width of major manus more than one-half length, one or both chelipeds broad and flattened 7
   Width of major manus less than one-half length; chelipeds subcylindrical ..... *longicarpus*
7. Width of major manus at least three-fourths length; right cheliped well developed, manus broad, flat, white; left cheliped scarcely different in size from preceding pereiopod. Eyestalks and antennules ringed with black .... *operculatus*
   Width of major manus only two-thirds length; both chelipeds broad and flattened 8
8. Movable dactyl of major manus with sharply produced angle on medial margin; no depressed spot at base of either immovable dactyl of chelipeds ..... *pollicaris*
   Movable dactyl of major manus with no sharply produced angle on medial margin; depressed spot at base of immovable dactyl of each cheliped .... *impressus*

Pagurus longicarpus Say, 1817

Fig. 13

Pagurus longicarpus Say, 1817: 163; Hay and Shore, 1918: 411; Wass, 1955: 152.

Eupagurus longicarpus, Gould, 1841: 330; Alcock, 1905: 182.

Diagnosis. Length of eyestalk not more than three and one-half times greatest width; width of major manus less than one-half total length; chelipeds subcylindrical.

Description. Chelipeds unequal, right much larger than left, major cheliped devoid of hairs except for a few very short setae along inner edges of fingers, tips of which are calcareous and acuminate. Length of movable dactyl less than

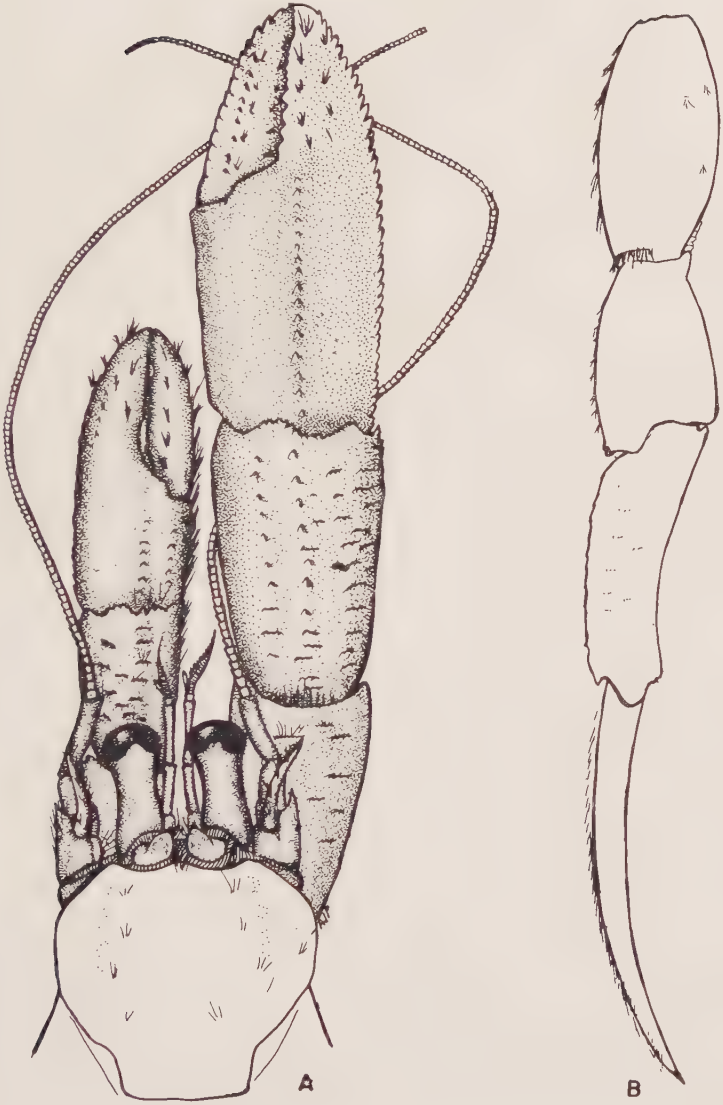

FIGURE 13. *Pagurus longicarpus* Say, 1817, x 5. A. Anterior body. B. Second left ambulatory leg.

half total manus length. Surface of manus covered with fine granules, a median ridge along upper surface. Carpus of major cheliped covered with fewer but larger granules; ridge continuous with that of manus carries forwardly projecting raised and enlarged granules. Minor cheliped more coarsely granulated, finger tips spooned, corneous.

Ambulatory legs with dactyls much longer than propodi.

Anterior carapace about as broad as long. Rostrum obsolete, not in advance of lateral projections.

Eyestalks widened at cornea, only 2-3 times longer than broad, much shorter than width of anterior carapace. Ophthalmic acicles with widely grooved, oval, anterior lobe, armed with subterminal spine.

Antennular peduncles exceed cornea by almost half length of last segment.

Antennal peduncles exceed cornea by about one-third length of last segment. Acicles reach to tip of cornea. Antennae exceed tip of major cheliped.

Color. The upper surface of all walking legs and the chelipeds is iridescent and this is noticeable even in preserved specimens. However, the color and to some extent the color pattern varies in this species as in *P. pollicaris* according to which part of the range the specimen is taken from. Specimens from the eastern Atlantic coast in general are much darker, and greenish-gray to brown in overall color, whereas those from the west coast of Florida are much lighter, with proportionally less pigment and more white area. Clearwater Beach specimens were as follows: posterior carapace light green. Ambulatory legs with dactyl unstriped, propodus with diffused lateral stripe, merus with single lateral muddy brown stripe and transverse stripe from lower anterior margin to broad pigmented area on upper surface. Manus white with median diffused pigment stripe, carpus with dorsal stripe and one on each side. Antennae with dark bands alternating with shorter white bands. Young may have transverse band on each ambulatory segment rather than stripe. Lateral stripes of major carpus give "V" appearance when viewed from above.

Size. L.c. male, 10 mm; female, (ovig.) 11 mm.

Range. Massachusetts southward to northern Florida, west coast of Florida from Sanibel Island north to Alligator Harbor, probably Gulf States. Alcock lists Brazil.

Type locality. East coast of United States?

Type. Not traced.

Discussion. None.

Remarks. There is an apparent break in the distribution of this species at southern Florida. I have seen specimens at Jacksonville, but not so far south as Miami, nor in the keys. The westward limit and the southward limit (except for Sanibel Is. northward) are undefined. Alcock's listing of Brazil is presumably taken from one of the authors he lists for the species. It would be very interesting to examine Brazilian material for, so far as I am aware, the species has not otherwise been reported south of the United States.

Material. 5 ovig. females and 19 other specimens; Sanibel Is., Fla., March 1938. Fenner A. Chace, Jr. MCZ 10147.

1 male; Seven Pines, s. side of Manatee River, Fla. 19 Feb. 1957. J. Murdock and A. Volpe. UMML 32: 1075.

2 males; Goose Cove, Cedar Key, Fla., Jan. 1942. R. W. Foster. MCZ 12056.

Numerous specimens; Clearwater Beach, Fla., among floating detritus on bottom near pilings, 17 May 1958. Provenzano.

Numerous specimens; Martha's Vineyard, Mass. July, Aug., Sept. 1958. Provenzano.

Pagurus operculatus (Stimpson, 1862)

Fig. 14

Eupagurus operculatus Stimpson, 1862: 92, pl. 1, figs. 9, 10.

Diagnosis. Length of eyestalks less than three and one-half times width. Major manus broadly oval, width at least three-fourths length, nearly flat, devoid of pigment dorsally. Left cheliped not conspiculously wider than preceding pereiopod. Cephalic appendages except antennae ringed with black.

Description. Chelipeds unequal, right very much larger than left. Major manus broadly oval from above, lacking pigment, hairs, or spines. Edges of hand flattened, upper surface covered with minute granules. Dactyl with longitudinal groove on upper surface. Carpus with inner margin bearing low, forwardly projecting spines, outer margin smooth. Granules on upper surface of carpus. Joint between manus and carpus usually with a fringe of flesh on ventral side. Major merus with 1-3 spines at antero-dorsal margin. Minor cheliped reaches to base of major dactyl, is much reduced in size, with finger tips corneous, spooned. Row of spines along each upper margin of carpus.

Anterior carapace longer than broad. Rostral projection rounded, slightly in advance of laterals.

Eyestalks moderately stout, shorter than front, slightly swollen at cornea. Ophthalmic acicles with slender, longitudinally grooved anterior lobe, acuminate.

Antennular peduncles reach easily to tip of cornea.

Antennal peduncles exceed eyestalks. Acicles simple, slender, outward-curving, reaching past base of cornea.

Ambulatory legs smooth, dactyls much shorter than propodi, with distinct row of spines along inferior margins. A few short hairs on upper surface of legs.

Color. In life the animal is very brilliantly and characteristically colored. The ambulatory legs and minor cheliped are orange without other colors or markings. The major manus is white above and nearly all white below, but the carpus and merus are maroon with white spots or blotches. The eyestalks, antennular peduncles, antennal acicles and peduncles are all banded with dark maroon and the edges of the anterior carapace have some patches of the same color. The antennae are orange.

Size. L.c. male, 11 mm; female, 8 mm.

Range. The Florida Keys, including Tortugas.

Type locality. "The Tortugas, Florida."

Type. Not traced.

Discussion. Of the 14 specimens in the USNM in April 1958 labelled *P. operculatus,* only one agreed with the original description and with the other specimens collected during this study. The others differ from

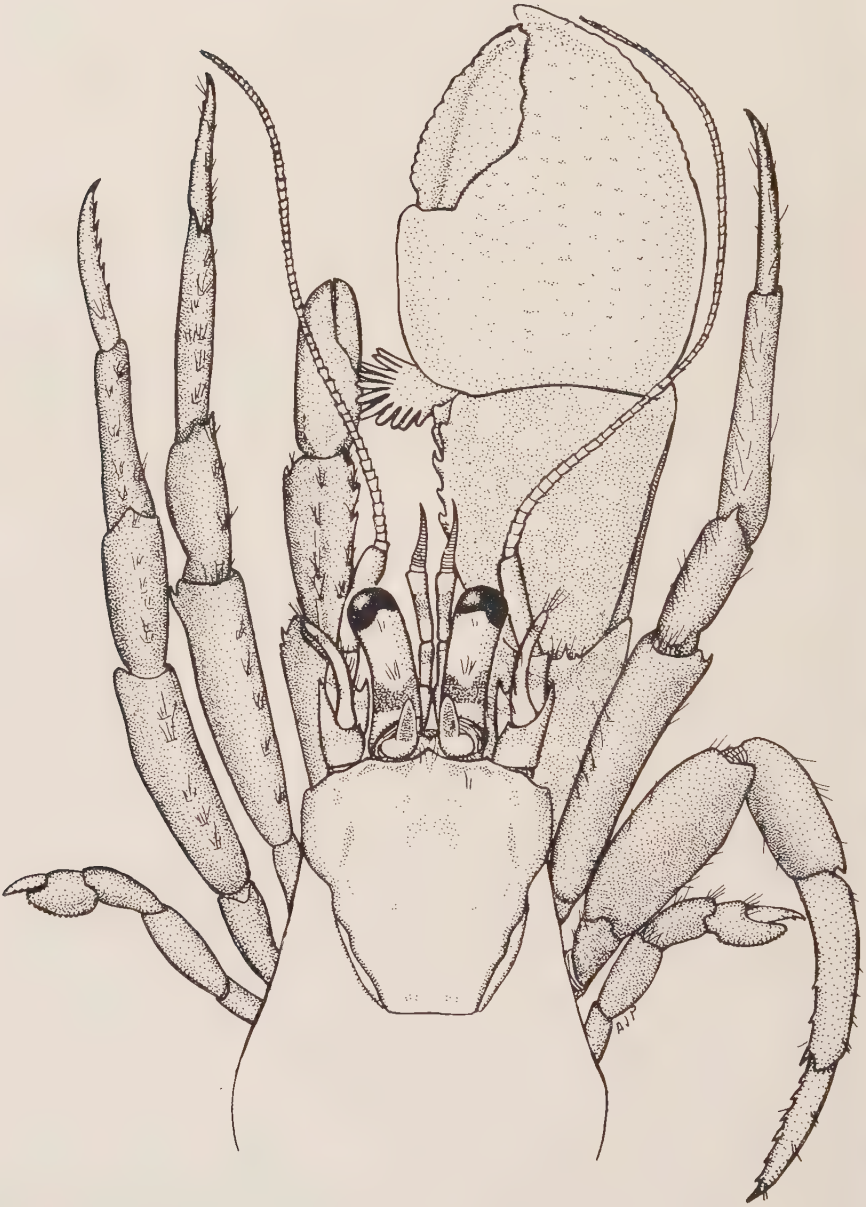

FIGURE 14. *Pagurus operculatus* (Stimpson, 1862).

Stimpson's species in having the propodi shorter than the dactyls in the ambulatory legs. There are other differences also, such as degree of spination on the major manus, the typical Stimpson "operculatus" having only granulations, whereas the others had very distinct spines. The single specimen which agreed with the description and the recently collected material from the keys was from a reef environment, as were nearly all the Fla. Key specimens taken during this study. Yet all the atypical USNM specimens were from deeper water (18-46 fathoms), from the Mississippi delta to North Carolina. Since it is highly unlikely that even such a different environment as these two groups inhabit could so radically affect the morphology of individuals, it is apparent that two species are involved. The identity of the deeper water specimens is unknown at this time, but there can be no question that the shallow water specimens belong to Stimpson's species. Accordingly, only shallow water material was used in working up the present description and illustration. The illustrated rostrum is exaggeratedly sharp; in most of the material it is decidedly obtuse.

The significance of the fleshy fringe between the manus and carpus of the major cheliped is not known at this time.

Remarks. None.

Material. 1 non-ovig. female; Bear Cut, Biscayne Bay, Fla., 29 June 1957. H. Kumpf. UMML 32: 813.
1 male; Long Reef, Fla., July 1957. R. Manning.
1 male; Long Reef, Fla., 19 April 1958. G. Shinn.
2 non-ovig. females; Long Reef, Fla., 29 June 1958. G. Voss.
1 male; Largo Dry Rocks, Fla., 9 Aug. 1958. G. Voss.
1 male; Carysfort Light, off Key Largo, Fla., 14 Aug. 1948. D. Moore and F. Lyman. USNM 88054.
1 specimen; rocks of MacArthur Causeway, Biscayne Bay, Fla., Feb. 1958. R. Work. To be deposited in USNM.

Pagurus impressus (Benedict, 1892)

Fig. 15

Eupagurus impressus Benedict, 1892: 5.
Pagurus impressus, Wass, 1955: 152.

Diagnosis. Length of eyestalk not more than three and one-half times greatest width. Width of major manus more than one-half length; both chelipeds broad and flattened. No sharply produced angle on medial margin of movable dactyl of major manus. Depressed spot at base of immovable dactyl of each cheliped.

Description. Chelipeds unequal, right much larger than left, both broad and flattened. Upper surface of each manus

> covered with granular plates, making a nearly even surface above the true surface. There is a depression near the outer margin opposite the base of the dactyl, and another running from the carpus nearly to the gape of the fingers in each hand.—Benedict.

Outer margin of major manus arcuate, set with blunt teeth. Carpus of major cheliped with prominent spines irregularly placed along outer margin, prominent teeth between base of dactyl and joint of carpus. Minor carpus more setose than major, but not obscuring surface at all. Two rows of very prominent spines along inner upper margin of carpus.

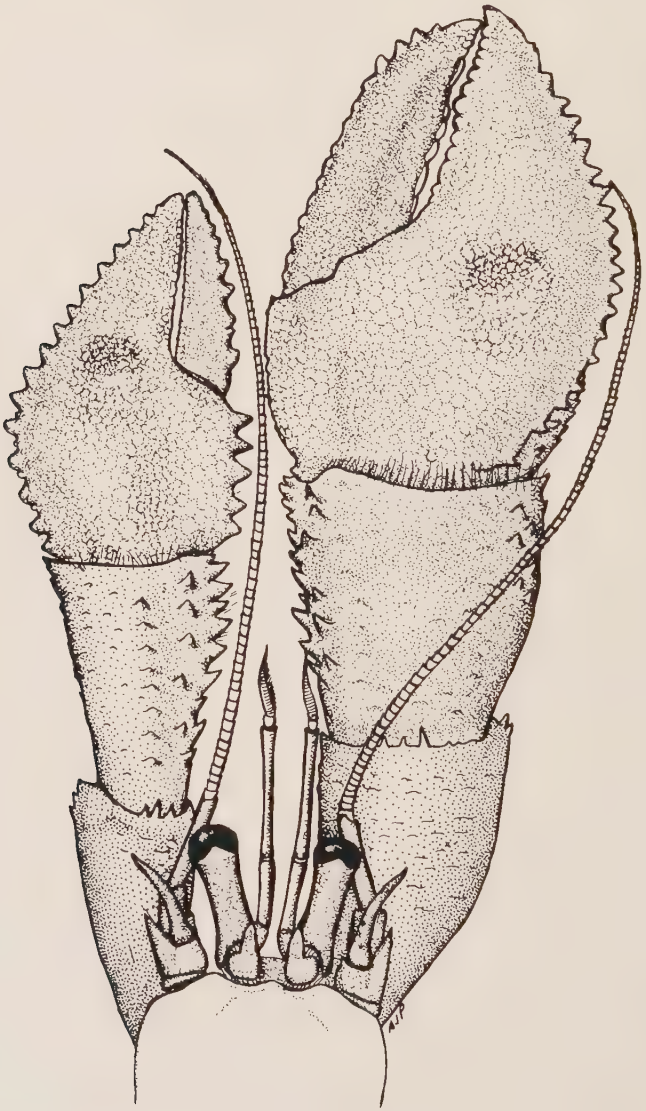

FIGURE 15. *Pagurus impressus* (Benedict, 1892) x 2.5.

Ambulatory legs sparsely hairy, dactyls longer than propodi. First pair with row of prominent spines along upper margin of propodus and carpus, but second pair only with much reduced spines on upper margin of carpus.

Anterior carapace about as broad as long, with rostrum rounded and in line with lateral projections which are somewhat more angular.

Eyestalks slightly swollen at cornea, about 3 times longer than greatest width. Equal to more than half greatest width of anterior carapace. Ophthalmic acicles with moderately slender, acuminate, slightly grooved anterior lobe.

Antennular peduncles exceed eyestalks by half last segment.

Antennal peduncles exceed eyestalks little if at all. Acicles curving gently outward reach to base of cornea, hairs along medial margin. Antennae exceed chelipeds.

Color. Hands solid rust to chocolate-brown, other appendages brownish with alternating thin bands of light color. Antennae, antennules and peduncles yellow. Eyestalks brown above, bright blue below with bright scarlet at very base of eyestalks.

Size. L.c. male, 21 mm; female, 15 mm.

Range. West coast of Florida from Sanibel Island north to vicinity of Alligator Harbor.

Type locality. Florida.

Type. On deposit in USNM.

Discussion. This species seems to be closely related to *P. pollicaris*. So far as I am aware, it is restricted to west Florida.

Remarks. None.

Material. 2 males; Blind Pass, Sanibel Is., Fla., 22 & 28 March 1938. F. A. Chace, Jr. MCZ 10149.

1 young female; Sea Horse Key area, Fla., on grass flat, 15 Sept. 1957. M. Wass.

Numerous specimens; Clearwater Beach, Fla., on sand among drifting detritus and pilings, 17 May 1958. Provenzano. To be deposited in UMML.

Pagurus pollicaris Say, 1817

Fig. 16

Pagurus pollicaris Say, 1817: 162; Hay and Shore, 1918: 411, pl. 30, fig. 1.
Eupagurus floridanus Benedict, 1892: 5.
Eupagurus pollicaris, Alcock, 1905: 182.
Pagurus floridanus, Wass, 1955: 152.

Diagnosis. Length of eyestalk not more than three and one-half times greatest width. Both hands broad and flattened, width of major manus more than one-half length. Movable dactyl of major manus with sharply produced angle on medial margin.

Description. Chelipeds unequal, right much larger than left, both covered with small granules in close contact. Outer margins bearing enlarged granules or small spines. Inner or medial margin of major movable dactyl with sharply produced angle. Finger tips of major cheliped acuminate, calcareous. Major

carpus with 5 longitudinal rows of small spines, often obscured by presence of irregularly arranged additional spines. A row of well developed spines along inner margin of carpus. Finger tips of minor manus somewhat spooned, at least with well defined cutting edge, tips corneous. Row of conspicuous spines along inner margin of hand. Manus itself reaches to produced angle on major movable dactyl. Minor carpus with several rows of small spines, a row of well developed ones along inner, dorsal margin.

Ambulatory legs with dactyls much longer than propodi. First pair with row of small but well defined spines along upper margin of propodus and carpal joint. Second pair with these reduced.

Anterior carapace about as long as broad, rostral projection rounded, not in advance of lateral projections from which front slopes backward rather sharply to lateral margins of anterior carapace.

Eyestalks moderately short and stout, not as long as width of anterior carapace. Much widened at cornea and flattened dorso-ventrally. Ophthalmic acicles with round-tipped slightly grooved anterior lobe armed with inferior subterminal spine.

Antennular peduncles exceed cornea by half length of last segment.

Antennal peduncles slightly exceed cornea. Acicles reach to base of cornea, are simple outward-curving, with hairs on medial edge.

Color. Color varies with locality (see Discussion) but west Florida specimens are as follows: chelipeds basically white with gray margins on the insides, tips of dactyls and dark pigmented area in center of upper surface of each cheliped. Rest of body light gray-tan. Brown pigment for short distance just below cornea. No stripes on legs, dactyls greenish distally. Hairs on antennules rusty brown.

Size. L.c. male, 25 mm; female, 16 mm.

Range. Massachusetts south to Georgia and even north-eastern Florida. West Coast of Florida from Key West north to Alligator Harbor, Gulf states to Texas.

Type locality. East coast of United States?

Type. Not traced.

Discussion. Benedict, in describing his new species, *Eupagurus floridanus,* separated it from *pollicaris* on the basis of narrower hands, produced angle of the dactyl being closer to the base, and the bordering granules of the outer margin of the hand being not so prominent, the outer margin itself being less rounded than in *pollicaris.* After examining his type, which is a relatively large specimen, and comparing material from the west coast of Florida with specimens from the eastern Atlantic states, I conclude that *floridanus* is not a distinct species. The narrower hands are apparently due to growth changes, but there is variation in this feature even among animals of similar size. Likewise the shape of the hand and prominence of marginal granules are unre-

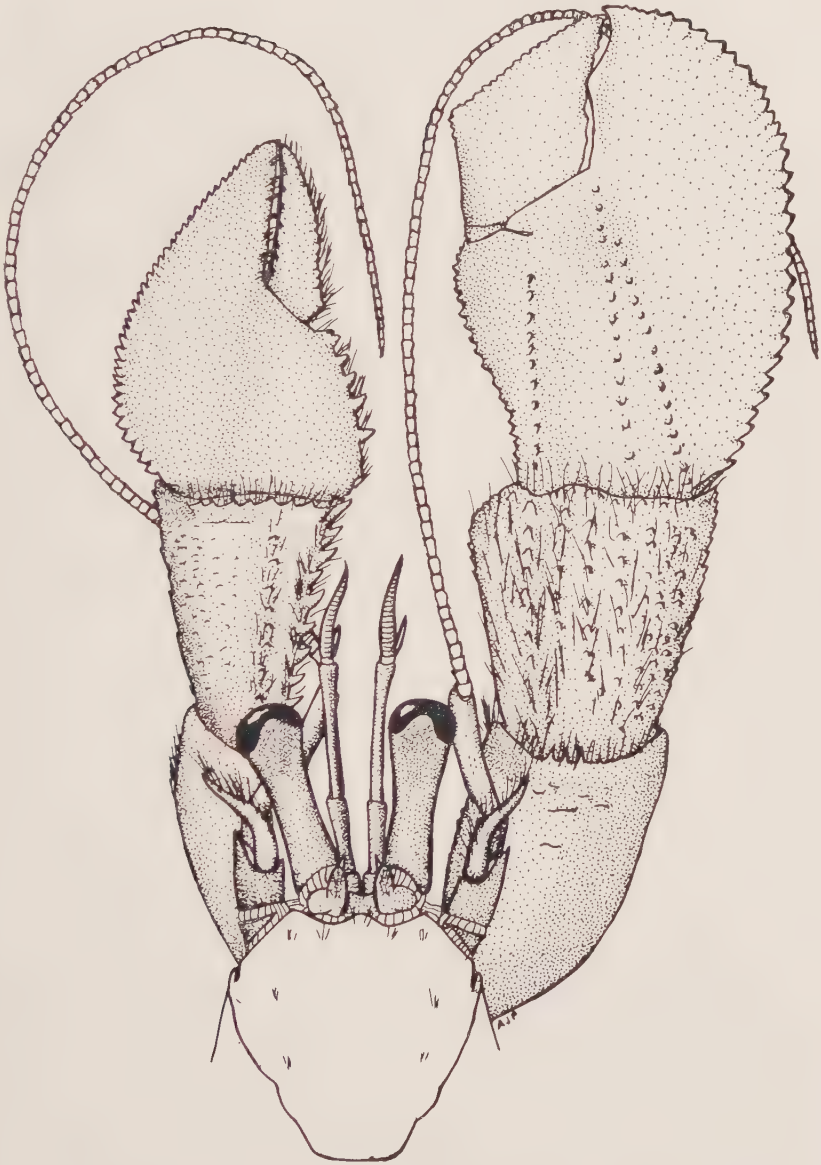

FIGURE 16. *Pagurus pollicaris* Say, 1817, x 4. A Sanibel Island, west Florida specimen.

liable characters to use in this particular case, varying within groups of individuals from any location. The lower position of the angle of the dactyl shows some tendency to predominate in specimens from west Florida, but some specimens from Massachusetts and elsewhere also differ from the more usual in having this angle lower than the midpoint of the dactyl. All fresh material (and even preserved specimens retaining any color at all) from west Florida and the Gulf of Mexico possess on the hands a coloring and color pattern different from the red-brown of Massachusetts specimens. In the west Florida material the hands were very light, especially the dactyls, but a dark pigmented area occupied the central, posterior portion of each hand. Although the differences stated by Benedict do not seem to warrant recognition of his *floridanus* as a distinct species, it is likely, in view of the break in distribution at south Florida and the constancy of color pattern in specimens from each side of the Florida peninsula, that the two populations represent subspecies. A similar situation exists in *P. longicarpus* Say.

Remarks. Perhaps in part because of the efficient closure of the shell by the chelipeds upon retraction, this species is much more conservative in its behavior after being disturbed than its more aggressive subtidal companion, *P. longicarpus*. Experiments in comparative behavior of morphologically similar and dissimilar members of the same genus might yield interesting results.

Material. Type of *E. floridanus* Benedict; Charlotte Harbor, Fla., March 1887, W. H. Dall. USNM 12448.

1 spec.; Lemon Bay, Fla., B. Hanstrom. 1 Nov. 1935. USNM 77425.

6 spec.; Cedar Keys, Fla., Dec. 1883. H. Hemphill. USNM 6448.

4 spec.; Little Gasparilla Pass, Fla., 7 March 1889, *Grampus*. USNM 16933.

1 spec.; Galveston, Texas, J. L. Baughman. USNM 81941.

1 ovig. female; Key West, Fla., U. S. Fish Comm. USNM 20237.

1 juv.; Key West, Fla., L. Agassiz & J. E. Mills. MCZ 12796.

1 male; Goose Cove, Cedar Keys, Fla., Jan. 1942, R. W. Foster, MCZ 12057.

1 ovig. female and 20 other spec.; Sanibel Is., Fla., March 1938. F. A. Chace, Jr. MCZ 10148.

1 non-ovig. female; off Currituck Sound, N. C. 18 meters, 8 April 1930, *Albatross II*. MCZ 11153.

1 non-ovig. female and 1 male; 3 July 1957, and numerous other specimens, July, August, Sept. 1958, off lobster hatchery, Lagoon Pond, Martha's Vineyard, Mass. Provenzano.

1 male; washed by storm into West Tisbury Great Pond, Martha's Vineyard, Mass., Jan. 1958. Provenzano.

5 females and 11 males; Sapelo Is., Ga. Oct. 1958, J. Teal.

Pagurus marshi Benedict, 1901

Fig. 17

Pagurus marshi Benedict, 1901: 139, text fig.; Schmitt, 1935: 205.

Diagnosis. Eyestalk length 5 times width. Movable dactyl of major manus one-half total manus length in male. Antennular peduncles do not extend beyond cornea. No pigment bands or stripes on ambulatory legs or on antennae. Ophthalmic acicles with single inferior or subterminal spine. Ambulatory dactyls not longer than propodi.

Description. Chelipeds unequal, right much larger than left, both covered with long fine hairs in rows corresponding to those of spines which are characteristically located, in major manus, in 6 rows, 2 very close together along each of upper surface margins, other 2 median, converging near gape of fingers. Six spines along inner margin of major carpus, others less conspicuous scattered on upper surface. Merus with slender spine above on anterior margin, two on each side of lower margin. Minor cheliped proportionally more slender than major. Well defined hiatus between fingers, which are spooned in contrast to acuminate finger tips of major manus. Spines distributed in rows, one along margin extending onto immovable fingers, double median row pointing to gape of fingers, and row crossing hand from base of movable finger onto immovable.

Ambulatory legs with dactyls not longer, usually distinctly shorter, than propodi. Dactyls with 6-9 ventrally placed spines in addition to tip. Carpus of first ambulatory leg with antero-dorsal spine and one dorsal but closer to body. Spines may be present on other segment of legs, which are covered with fine long hairs along margins.

Anterior carapace longer than broad. Rostral projection oval, in advance of laterals which may have terminal spine.

Eyestalks as long as front, 5 times longer than broad, curving outward at about mid-point. Ophthalmic acicles simple, slightly depressed in projecting portion, armed with subterminal spine.

Antennular peduncles about as long as eyestalks, exceeding them little if at all.

Antennal peduncles scarcely reach tips of eyestalks. Acicles unarmed, outward curving, slightly hairy, reaching about three-fourths length of eyestalks.

Color. Dirty white, with no pigment patterns in the material examined.

Size. L.c. male, 6 mm; female, 6.5 mm (ovig.).

Range. South Florida, Puerto Rico and Curacao.

Type locality. Ponce, Puerto Rico.

Type. On deposit in USNM.

Discussion. In describing *P. bonairensis,* Schmitt (1936) discussed the resemblances of the two species. It is unfortunate that *P. bonairensis* has not been reported since, for the type is apparently lost and a detailed comparison now impossible. However, from the literature, it seems that the principal distinguishing features which set the two species apart are the distinct rostrum in *P. marshi,* its corresponding absence in *bonairensis;* the extension of the antennular peduncles past the cornea in the latter species; and the pronounced differences in the

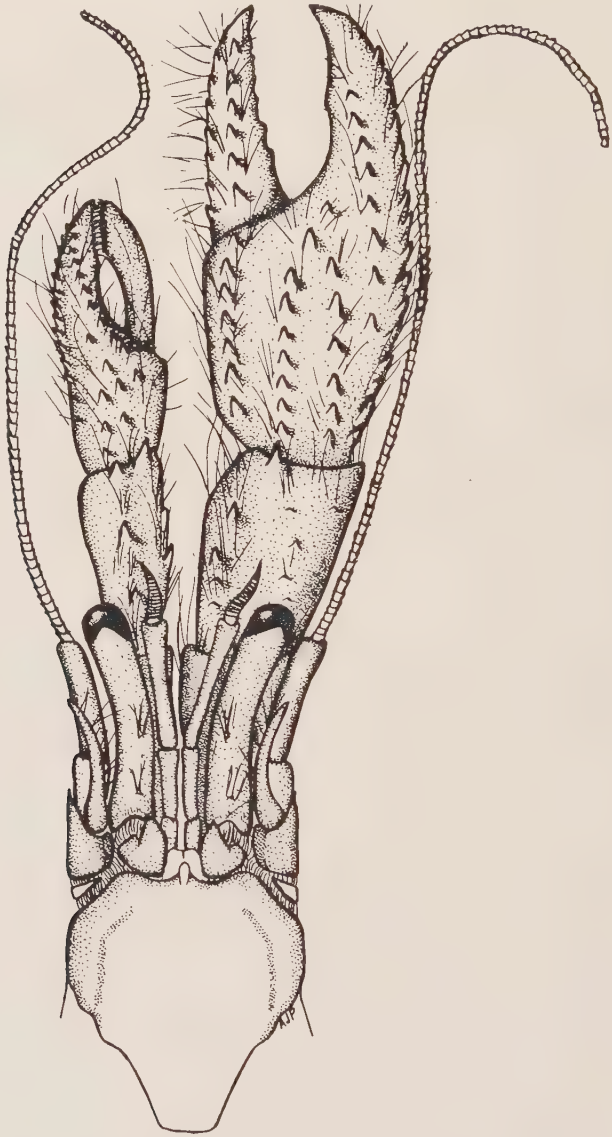

FIGURE 17. *Pagurus marshi* (Benedict, 1901), x 9.

chelipeds, both minor and major, the minor cheliped in *bonairensis,* for example, being reportedly triangular, and the major manus lacking one of the rows of spines present in *marshi.*

Remarks. This hermit is one of the least commonly found species in south Florida. It may prefer somewhat exposed localities where water circulation is good.

Material. 1 male; Bache Shoals, off S. end of Biscayne Bay, Fla., August 1957. R. Manning. UMML 32: 1073.

1 male; S. end of Long Key, Fla., ocean side, 19 Apr. 1957. Provenzano. UMML 32: 1072.

1 ovig. female; Bear Cut, Biscayne Bay, Fla., 29 Sept. 1956. Student field class. UMML 32: 1074.

Pagurus annulipes (Stimpson, 1862)

Fig. 18

Eupagurus annulipes Stimpson, 1862: 243.

Pagurus annulipes, Hay and Shore, 1918: 412, pl. 29, fig. 12; Schmitt, 1935: 206; Wass, 1955: 152.

Diagnosis. Eyestalk length 5 times width. Ophthalmic acicles armed only with subterminal spine. Dactyl of major manus less than one-half length of hand. Antennular peduncles extend well beyond cornea. Antennae with alternating bands of purple and white. Legs transversely banded with brown or purple on white. Ambulatory dactyls longer than propodi.

Description. Chelipeds unequal, right much larger than left. Major manus evenly granulated above except in large specimens where granules become small spines. Movable dactyl less than one-half length of hand, finger tips acuminate, calcareous. Major carpus nearly twice as long as broad. Minor cheliped slender, compressed, fingers with corneous cutting edges. Manus with spines much more prominent than on major manus. Carpus longer than manus, fingers longer than palm of hand. Double row of spines on carpus and manus obscured by hairs.

Ambulatory legs with dactyls longer than propodi. Legs slender, compressed. Carpus with spine at antero-dorsal margin.

Anterior carapace scarcely longer than wide. Rostral projection obsolete, not in advance of much rounded laterals.

Eyestalks nearly straight, shorter than front. Ophthalmic acicles flat, not acute, but usually armed with one or, rarely, two spines on anterior margin.

Antennular peduncles exceed eyestalks by about one-third of last segment.

Antennal peduncles may or may not reach tip of eyestalk. Acicles reach two-thirds length of eyestalk, curving slightly outward. Antennae exceed major cheliped.

Color. White to gray with brown pigment band around each segment of ambulatory legs. Antennae with broad purple bands alternating with narrower white bands. Occasional individuals may have very poorly defined longitudinal stripes on the leg segments.

Size. L.c. male, 5 mm; female, 3.8 mm.

Range. Massachusetts south to the Florida Keys, around the tip of Florida and northward at least as far north as Alligator Harbor, probably westward. Cuba and Puerto Rico.

Type locality. Beaufort, North Carolina.

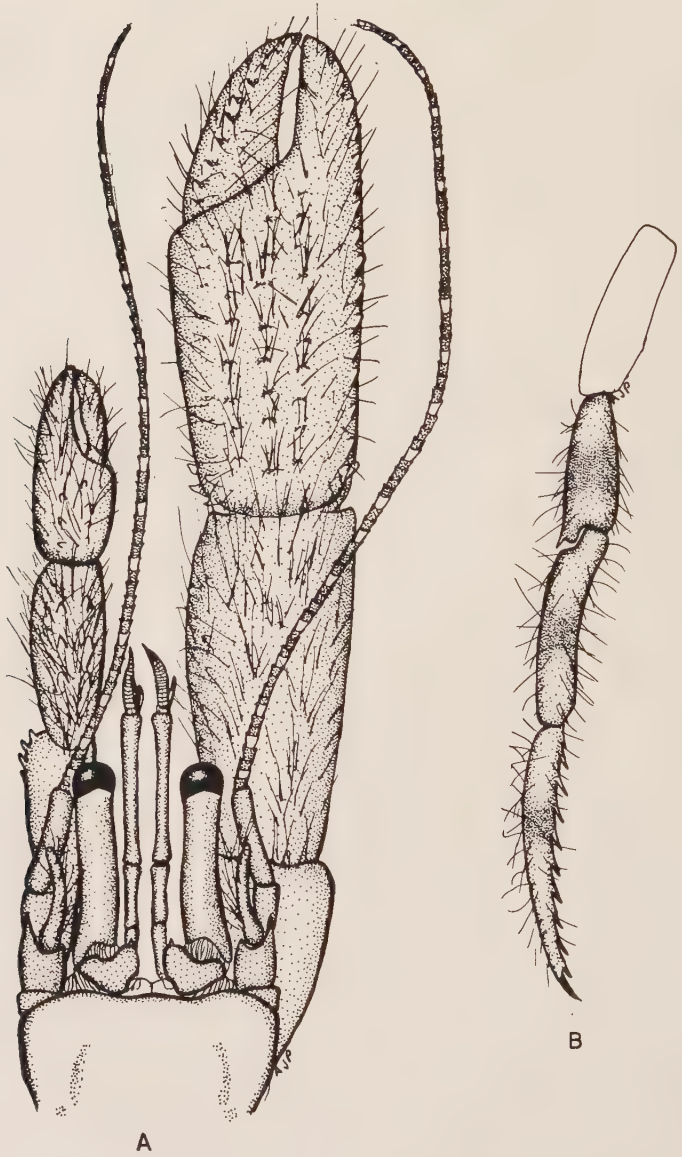

FIGURE 18. *Pagurus annulipes* (Stimpson, 1862), x 8. A. Anterior body. B. Lateral view of second left ambulatory leg showing characteristic pigment bands.

Type. Not traced.

Discussion. There could never be any difficulty in separating *P. marshi* and *P. annulipes,* yet both species have some features in common with Schmitt's *bonairensis.* As mentioned previously, it is most regrettable that lack of specimens prevents a detailed comparison of *P. bonairensis* with other members of the genus, but even with the brief description of that species we are able to tell it is somewhat allied to *P. annulipes.* The major difference in the front seems to be an absence in *annulipes* of readily discernible subapical spines on the lateral projections. The other principal features in which the two species differ seem to be the form of the minor manus (triangular in *bonairensis,* not so in *annulipes)* and the much more pronounced spination in *bonairensis* on the chelae. Whether these differences suffice to distinguish the two may not be known until more material resembling *bonairensis* becomes available, but it seems likely that Schmitt should have been able to distinguish the two.

Remarks. This species, like *P. longicarpus* and *P. pollicaris,* is found in shallow water all the way from Massachusetts to Florida and along the Gulf states. Unlike the others, however, it does not have a break in distribution at south Florida, but continues right around the Keys, in Florida Bay and northward. Apparently its tolerance to high temperatures in the southern part of its range allows it to extend even further south, for it has been reported from Cuba and Puerto Rico. The species is very abundant in *Thalassia* beds in south Florida and seems to prefer soft sandy bottom to other types of habitat, not minding even slightly reduced salinities.

In the material examined there was a definite tendency for males to attain larger size than females, and this larger size was accompanied by proportionally larger major cheliped.

Material. 1 ovig. female; Indian Key, Fla., 1 Feb. 1958. Provenzano.
10 spec.; Matheson Hammock, just south of Miami, 27 Jan. 1958. Provenzano. UMML 32: 379.
1 ovig. female and 1 male; North Key Largo, 21 April 1957. Provenzano.
3 ovig. females and 5 males; 2 mi. north of Jewfish Creek, Key Largo, 21 April 1957. Provenzano.
2 ovig. females and 4 males; Biscayne Bay, Fla., August 1937? J. F. W. Pearson. MCZ 9821.
2 ovig. females and 1 male; Matheson Hammock, 25 Sept. 1957. R. Manning.
10 ovig. females and 26 others of mixed sex; Bear Cut, Biscayne Bay, 9 Feb. 1958. Provenzano.
1 ovig. female and 7 other spec.; Matheson Hammock, 9 March 1958. R. Manning.

1 ovig. female and 9 other spec., two parasitized; Joe Kemp Channel, Fla. Bay, 11 March 1958. Durbin Tabb.

5 spec.; Gay Head, Mass., off Devil's Bridge, 70-80 feet, 30 Jan. 1958, Milton Gray. (MBL Supply Dept.)

Pagurus pygmaeus (Bouvier, 1918)

Fig. 19

Eupagurus pygmaeus Bouvier, 1918: 11, fig. 4.

Diagnosis. Eyescales armed with 4-5 spines on medial margin. Rostrum acute. Dactyls of ambulatory legs shorter than propodi. No stripes on legs.

Description. Chelipeds unequal, right much larger than left. Major manus suboval, armed with very strong forward-projecting spines along each margin. Upper surface of manus covered with smaller, nearly blunt forward-projecting spines. Major carpus with 6 very sharp forward-projecting spines on upper anterio-medial surface, 2 additional spines more laterally placed, and a short row of spines along lateral margin. Minor manus much reduced, twice longer than broad, finger tips corneous, spooned. Upper surface with many blunt spines, some of which form two central rows. Carpus with double row of large forward-projecting spines on upper surface. Both chelipeds with long, but very fine, hairs.

Ambulatory legs with dactyls shorter than propodi, carrying about 5 ventrally placed spines in addition to terminus. Propodus with about 7, but less conspicuous. Long setae on all segments, but not obscuring surfaces.

Anterior carapace longer than wide, rostrum acute, slightly in advance of lateral projections which have a terminal spine.

Eyestalks shorter than width of anterior carapace, wide at base, tapering towards cornea. Ophthalmic acicles with elongate anterior lobe armed along medial margin with 4-5 spines.

Antennular peduncle slightly exceeds cornea, flagellum longer than last peduncular segment.

Antennal peduncle also exceeds cornea; unarmed acicle reaches base of cornea. Antennae exceed major cheliped.

Color. Only color present in the specimen at hand, other than a pink cast on the major manus, is a diffusely pigmented area at the distal end of each ambulatory segment.

Size. L.c. male, 3.1 mm.

Range. Known only from type locality and Long Reef, Fla.

Type locality. La baie de la Zocappa near Santiago de Cuba.

Type. Apparently missing from the collections at Paris (J. Forest, personal communication).

Discussion. The feature of armed ophthalmic acicles is shared with the two species next discussed, as are the short dactyls of the ambulatory legs, but the acute rostrum, and especially the character of the chelipeds immediately sets this species apart from them. Bouvier's female had an over-all length of only 1 cm., hence the name.

Material. 1 male; Long Reef, Fla., 29 June 1958, Gilbert L. Voss. UMML 32: 1135.

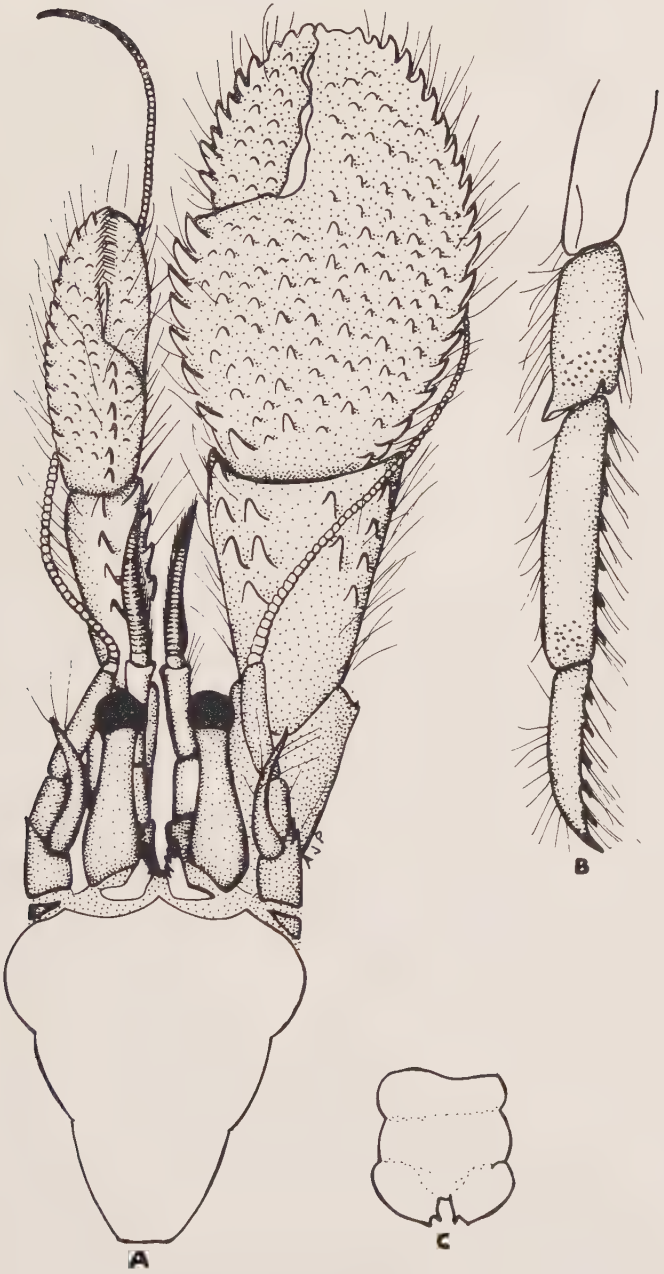

FIGURE 19. *Pagurus pygmaeus* (Bouvier, 1918)., x10 A. Anterior body. B. Second left ambulatory leg. C. Telson.

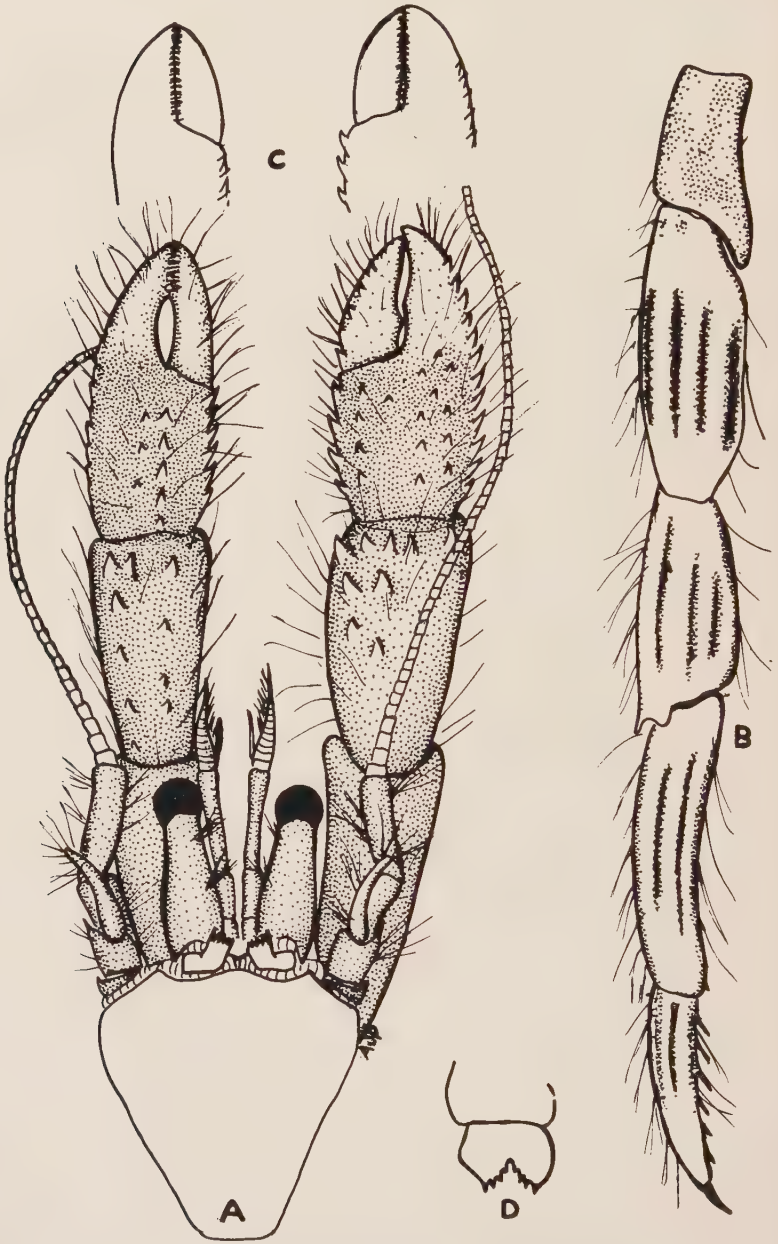

FIGURE 20. *Pagurus brevidactylus* (Stimpson, 1862)., x8 A. Anterior body of male specimen. B. Second left ambulatory leg. C. Outline of chelipeds of female showing similar nature of inner margins. D. Telson.

Pagurus brevidactylus (Stimpson, 1862)

Fig. 20

Eupagurus brevidactylus Stimpson, 1862: 91.

Diagnosis. Eyescales truncate rather than acuminate, armed with 4-6 spines along anterior margin. Rostrum obsolete. Eyestalks wide at base, tapering towards cornea. Dactyls of ambulatory legs shorter than propodi. Interrupted red stripes on each leg segment.

Description. Chelipeds equal or subequal (in females), finger tips corneous, spooned. Chelipeds unequal in males, right larger. Outside margins of both hands edged with spines. Smaller spines in several rows on upper surface of hands. Carpus of each cheliped with strong spines on upper surface. Hands with fine hairs.

Ambulatory legs with dactyls shorter than propodi. Dactyls with 5-8 conspicuous spines along inferior margin. Propodi with only 1-2 inconspicuous spinules along inferior margin. Legs with long but fine inconspicuous hairs.

Anterior carapace very slightly longer than broad. Rostrum obsolete, about on line with lateral projections.

Eyestalks swollen at base, tapering towards cornea, giving characteristic stoutness even in fully adult specimens. Ophthalmic acicles armed along anterior border with 3-6 spines.

Antennular peduncles reach at least to tips of eyestalks.

Antennal peduncles slightly exceed eyestalks. Acicles reach to base of cornea or slightly beyond.

Color. Very characteristic color pattern on leg segments consists of a total of 6 rust red or maroon stripes on propodus, carpus and merus, fewer on dactyls. Stripes run longitudinally and are interrupted, that is, do *not* reach the entire length of each segment, but end before the joints are reached. Background color on leg segments is yellow. The hands are brown with nearly completely white fingers, not striped. No distinct stripes on carapace which has a scattering of red and white pigment in fresh material.

Size. L.c. male, 3.0 mm; female, 4.1 mm.

Range. Known from Miami, Fla. northward as far as North Carolina, as well as Barbados. Presumably to be found throughout the West Indies.

Type locality. Barbados.

Type. Not traced.

Discussion. Although Stimpson's description lacked many details and he did not illustrate his species, it is felt that the material at hand does belong to his (*Eu-*) *Pagurus brevidactylus,* for the characteristic interrupted red stripes which he mentioned have not been found on any other West Indian littoral hermit so far as I am aware. The other general features discussed by Stimpson, even to the small size and the

habitat, agree fairly well, but in the original description the eyestalks are said to be very long and slender. This need not be too serious a discrepancy, however, for compared to the other, short-eyestalked species of the same genus which he also discussed in the paper, the eyes of this species are indeed relatively long.

Remarks. There is a sexual dimorphism in this species as in certain others, in the form of the chelipeds. In females, the hands are much more nearly the same size, and the right is also spooned and serrate along the inside margins of the fingers, whereas, in males, the right hand not only gets slightly larger, but the fingertips appear more acuminate and the inside margins of the fingers each bear a tooth.

The species seems to prefer areas of fairly good circulation, and a hard bottom.

Material. 1 non-ovig. female; off Jade House, north of Lauderdale-by-the sea, Fla., 15 ft., sandy but rocky bottom. 15 April 1958. Provenzano and A. Lewis.

4 ovig. females; 12 April 1958.

1 ovig. female and 1 male; 20 April 1958.

11 ovig. females and 2 males; 5 May 1958, all from Government Cut, Miami Beach, Fla., on rocks, 5-10 ft. Provenzano.

1 male; Virginia Key, Fla., 22 April 1958. R. Work.

1 ovig. female; 19 June 1949, USNM 89623; 1 ovig. female, 7 July 1949, USNM 90073; 1 ovig. female, 8 August 1949, USNM 90074. All collected at Black Rocks off New River, North Carolina, by A. S. Pearse.

Pagurus miamensis, n. sp.

Fig. 21

Diagnosis. Eyescales truncate, armed with 3-6 spines along anterior margin. Rostrum obsolete. Eyestalks about as long as front. Dactyls of ambulatory legs not longer than propodi. Leg segments with longitudinal stripes not interrupted, but reaching from one joint completely to the next; a total of 5 such stripes on propodus.

Description. Chelipeds subequal, or unequal, right larger than left, especially in larger males. Finger tips corneous, spooned. Double row of white spines on upper surface of major movable dactyl. Inner margin of major manus armed with similar spines, other arranged less regularly on upper surface of manus. Major carpus with 6 spines on inner margin, about 11 elsewhere on upper surface. Merus with single large white spine at antero-dorsal margin, 1-2 spines on exterior lower margin. Minor cheliped with double row of white spines on outer margin of hand, single row on upper surface of manus. Minor carpus with 4 spines on outer, 2 on inner margin. Merus with 5-6 spines on outer, 2 on inner inferior margins.

Ambulatory dactyls shorter, or at least not longer, than propodi. Six to seven spines on inferior margins of dactyls, 3 spines on anterior inferior margin of propodus. Single white spine on antero-dorso margin of merus. Lateral surface smooth except for fine hairs.

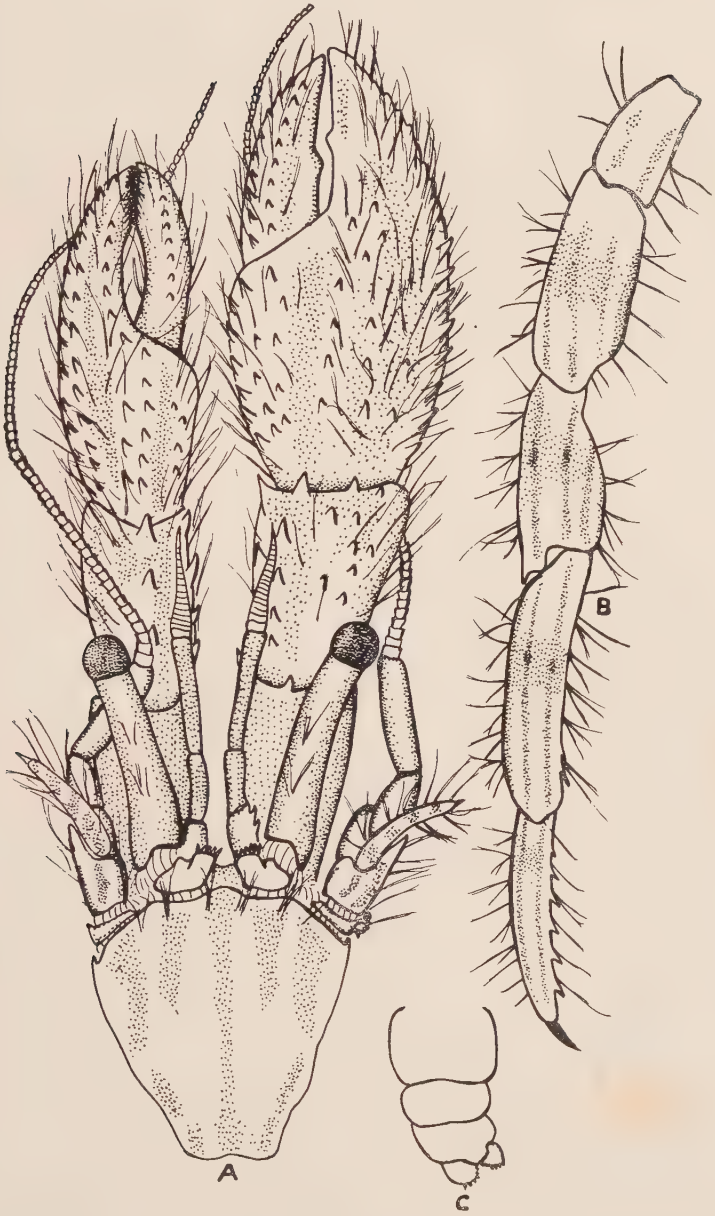

FIGURE 21. *Pagurus miamensis* n.sp., x10. Holotype. A. Anterior body. B. Second left ambulatory leg. C. Telson.

Anterior portion of carapace as long as wide, rostrum obsolete, but in advance of lateral projections.

Eyestalks as long as front, in adults 4-5 times longer than greatest width. Ophthalmic acicles broad, truncate, not elongate, and with 3-6 well developed anterior marginal spines.

Antennular peduncles reach tip of cornea:

Antennal peduncles nearly reach tip of cornea. Acicles simple, outward curving, armed with large terminal spine.

Color. Predominant color of markings may be green, rust-red, or purple. Ambulatory legs longitudinally striped on each segment, stripes extending entire length of each segment and darker in region of faint transverse pigment band on each segment. Chelipeds faintly striped longitudinally, not solid brown with white fingers. Carapace with medial and lateral stripes on light background. Eyes pink with pinkish stripe on upper surface of eyestalks, dark on under surface. Antennules pigmented. Antennal acicles mottled; antennae with alternating dark and light bands.

Size. L.c. male, 5.5 mm; female, 3.0 mm.

Range. Known at present only from Bahamas and Miami, Fla. area.

Type locality. Government Cut breakwater, Miami Beach, Florida, 5-10 ft. on rocks.

Type. Male holotype, USNM Cat. No. 102456 collected 12 April 1958 at type locality in company with 5 other specimens. (For allotype and paratypes see "Material.") Holotype measurements: front to telson, 16 mm; L.c. 5.5 mm; L. ant. carapace, 3.1 mm; width anterior carapace, 3.0 mm; eyestalk length from front, 2.7 mm; length of major manus, 5.0 mm; width of major manus, 2.6 mm; length of movable dactyl of major manus, 2.2 mm.

Discussion. The closest relative of this species among West Indian hermits is *Pagurus brevidactylus.* The two share the uncommon feature of well armed ophthalmic acicles with *P. pygmaeus,* but unlike that species, these have an obsolete rostrum and much more nearly equal chelipeds. All three species share the short ambulatory dactyls. As in *brevidactylus, P. miamensis* shows some variation with size and sex in the form of the right cheliped, but much more strongly. In females the hands are nearly equal, the tips rounded, corneous, spooned. In males, however, especially larger ones, the right hand becomes considerably larger than the left and appears more acuminate at the finger tips, than spooned like the left. The single teeth on the inside margin of each

major dactyl are present in this species as well as in the preceding. In fresh specimens the color patterns of *P. brevidactylus* and *P. miamensis* immediately set the two apart, despite the longitudinal striping in common, for in the former the stripes are interrupted and present on the legs only, whereas in *P. miamensis* the stripes reach the entire length of each segment and are also present on the carapace and elsewhere. In *P. brevidactylus,* moreover, the hands are brown with white fingers, while in the present species there is no such pattern to the hands. In preserved material it becomes more difficult to separate the two, especially when pigment is completely gone, but a number of features will allow distinction if care is given to details. In *P. brevidactylus* the eyestalks are rather broad throughout their length compared to those of other long-eyed species. In *P. miamensis,* as in most hermit crabs, the youngest specimens tend to have much shorter and thicker eyestalks than fully mature specimens, and these younger individuals may give some trouble, but in medium and large specimens, the long and slender eyestalks provide an easy means for separation of *P. brevidactylus* and *P. miamensis.* The former seems not to get as large as the latter, even when adult males are compared, and the more unequal chelipeds in adult males are another aid to separation of faded, preserved specimens. A comparison of telsons of a few specimens of each species seemed to show that in *P. miamensis* the spinules are smaller, although the numbers are similar, but whether this will prove a useful or reliable character is not known.

Remarks. Like *P. brevidactylus,* this species seems to prefer somewhat exposed, rocky bottom where good circulation is present.

Material. In addition to holotype, two ovig. females (one of which has been selected ALLOTYPE) and 3 males (paratypes) were collected on 12 April 1958; Government Cut Breakwater, Miami Beach, Fla., on rocks, 5-10 ft. Provenzano. USNM. 102457 and 102458.

Other paratypes: 4 ovig. females and one non-ovig.; 5 May 1958. 1 non-ovig. female and 1 male; 20 April 1958, all at type locality by author.

1 male; Bimini, Bahamas, 1 Nov. 1948, dredge 6 ft. A. S. Pearse. USNM 88641. (Paratype).

1 female; Bimini, Bahamas, 15 Oct. 1948. A. S. Pearse, USNM 88642. (Paratype).

1 ovig. female and 1 male; Bimini, Bahamas, 2 Nov. 1948. A. S. Pearse. USNM 88643. (Paratype).

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THE SETTLEMENT AND GROWTH OF *BALANUS IMPROVISUS*, *B. EBURNEUS* AND *B. AMPHITRITE* IN THE MIAMI AREA[1]

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ABSTRACT

Data for twelve years on the settlement, survival and growth of three species of barnacles in the Miami area are analyzed. Long period, seasonal and short period fluctuations are described, and the correlations of these with temperature and river discharge are discussed. In two of the species there appear to be three distinct spawning periods during the year, and it is possible that these coincide with the maturation of three successive generations since growth and maturation are very rapid.

INTRODUCTION

There is considerable information available on the abundance and growth of barnacles in relation to tidal level, wave action and food supply. The present study throws some light on the less well known effects of temperature and salinity.

A commercial marine paint testing station is maintained (by A.C.F.) at Miami Beach. Hela *et al.* (1957) have described the hydrography of Biscayne Bay, and the testing station lies between their stations 95 and 406, where the Venetian Causeway joins Miami Beach. It was moved there in November-December 1952 from a closeby location on Belle Isle, and tests at the time showed no significant difference in fouling between the two localities. The 8 by 10 inch test panels were at first glass, but about 1952 these were changed to formica which had been soaked in sea water for several months before use. Here also tests showed that no significant change in fouling was involved. The test panels are suspended at a depth of about two feet below low water. One panel is removed every day, a count made of the total barnacle settlement in the past 24 hours, and the panel is then scraped and returned to the water. Every month another panel is removed after one month exposure, a count made of the numbers of each of three species of barnacles, together with certain other fouling or-

[1]Contribution No. 242 from The Marine Laboratory, University of Miami.

ganisms, and a record made of the size range of each of the barnacle species. Daily sea temperature records are also kept. Over the twelve year period analyzed here there are, therefore, approximately four thousand observations of settlement of barnacles, not separated by species, and 144 records of both numbers and maximum size of each of the three *Balanus* species. It is unfortunate from the point of view of the present analysis that with one or two exceptions, no records of one month growth beyond 12 mm were made, thus eliminating information on summer growths which were usually above this value. However, the data available is so extensive that it justifies detailed analysis. Weiss (1948) has published an account of fouling at this station for the years 1943 to 1946.

Data on rainfall and wind were taken from the U. S. Weather Bureau summaries for Miami, but neither provided significant correlations. Salinity is largely dependent on the discharge from the Miami River. Monthly values for this are taken from Hela *et al.* (1957), and subsequently from information kindly provided by Mr. Hartwell of the U. S. Geological Survey. We are grateful to many members of the staff of The Marine Laboratory for helpful suggestions and criticism, and particularly to Miss A. Feinstein for statistical assistance.

Cypris Settlement

When the panels are examined at the end of 24 hours exposure, most of the cypris larvae have metamorphosed, but they are referred to here as cypris for convenience. No attempt was made to distinguish their species, and there is no information available as to possible difference in survival rate of the three species. For the whole period, *Balanus improvisus* constituted 80.7%, of the barnacles on the one month panels, *B. amphitrite* 12.5%, and *B. eburneus* 6.7%. The three showed very similar patterns of seasonal abundance, but varied somewhat from year to year in relative abundance. Assuming similar mortality rates, the counts on the 24 hour panels refer mainly to *B. improvisus*.

There is considerable long period fluctuation in the density of cypris settlement (Fig. 1). It may be assumed that the rate of settlement depends on both the numbers of larvae liberated and their survival rate while planktonic. The supply is a function of the number of adult barnacles in the area, no doubt modified by suitability of breeding conditions. There are no figures available on the numbers of barnacles in the area, but during the period there has been a steady increase in

FIGURE 1. Annual mean daily cypris settlement (O) per panel, and river discharge (X). The latter, derived from monthly data, is weighted in proportion to the settlement rate of cypris in that month.

FIGURE 2. Long period trend in the annual mean survival of all barnacles on the one month panels (O), including data from Weiss (1948), and population of Dade County (X).

human population, (Fig. 2) no doubt accompanied by a similar increase in docks, boats, and similarly hard surfaces suitable for attachment. There has been a parallel steady increase in total fouling as indicated by the one month panels. Survival of nauplii and cypris is probably a question of duration of the planktonic phase rather than of direct harm from unfavorable conditions. A shorter time in the plank-

ton means less predation and less chance of being carried out of the area by currents. Rate of larval development is likely to be modified by food supply and temperature in particular. The parallel between the fluctuations in river discharge and those in cypris settlement suggest that river born sediments and nutrients are a significant food source for the larvae. If this is the case, the difference in the general trends of the two lines will have to be accounted for by a long period increase in larval production as suggested above. This is at least a possibility, and

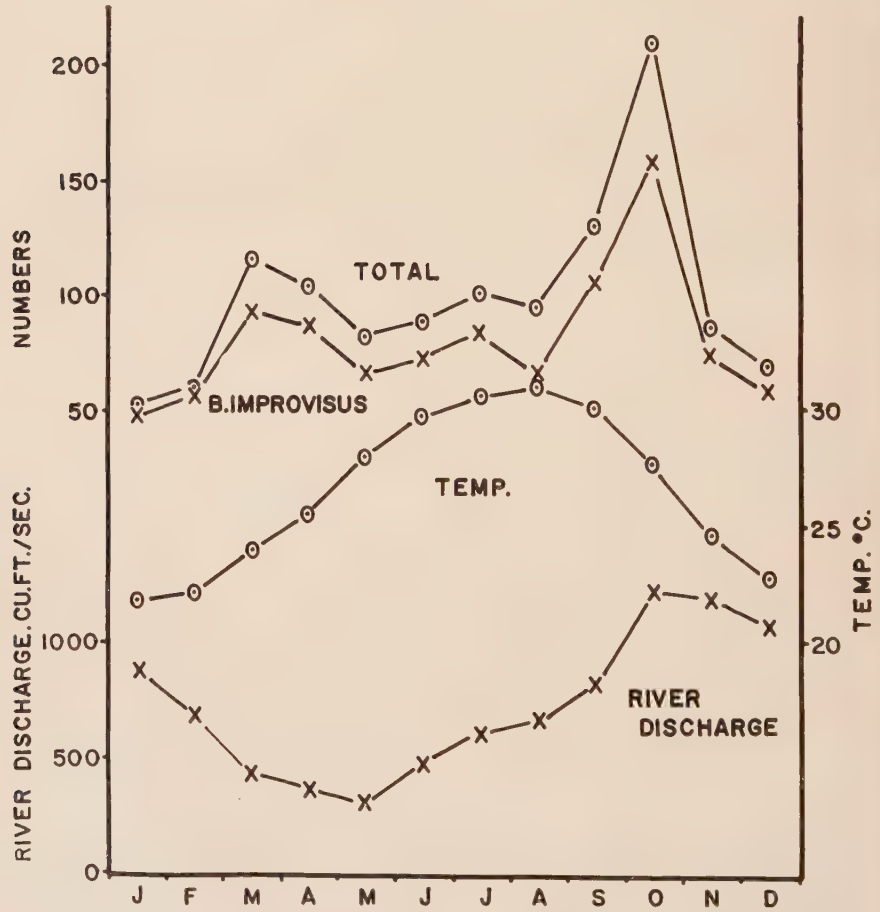

FIGURE 3. The seasonal settlement of cypris (O) after elimination of the effect of long period cycles, and the same values scaled in proportion to the percentage of *B. improvisus* among the total barnacles settling (X). Lower curves, the mean monthly values of temperature (O) and river discharge (X).

no other factor examined showed as close a correlation. Although temperature did not appear to be directly correlated with the long period variations in cypris settlement, it did prove to have some effect, as shown below. The values of river discharge used have been weighted in proportion to the mean seasonal variation in cypris settlement.

A method described by Shiskin (1958) has been used for distinguishing the long-period trends, seasonal cycles and short-period fluctuations. To remove the long period cycle and emphasize the seasonal cycle, a twelve month running mean was calculated. Each monthly mean was then divided by the corresponding running mean. Finally a twelve year mean for each month was calculated from the resulting figures. The result is shown in Figure 3. There are two definite peaks, in the spring and autumn, and a possible one in early summer. Later analyses showed a similar triple peak in two of the three species, but with some difference in the time of the peaks. *B. improvisus* constitutes the majority of the attaching barnacles, but its percentage varies somewhat seasonally. The seasonal settlement figures were therefore multiplied by the mean percentage of *B. improvisus* for that month. with

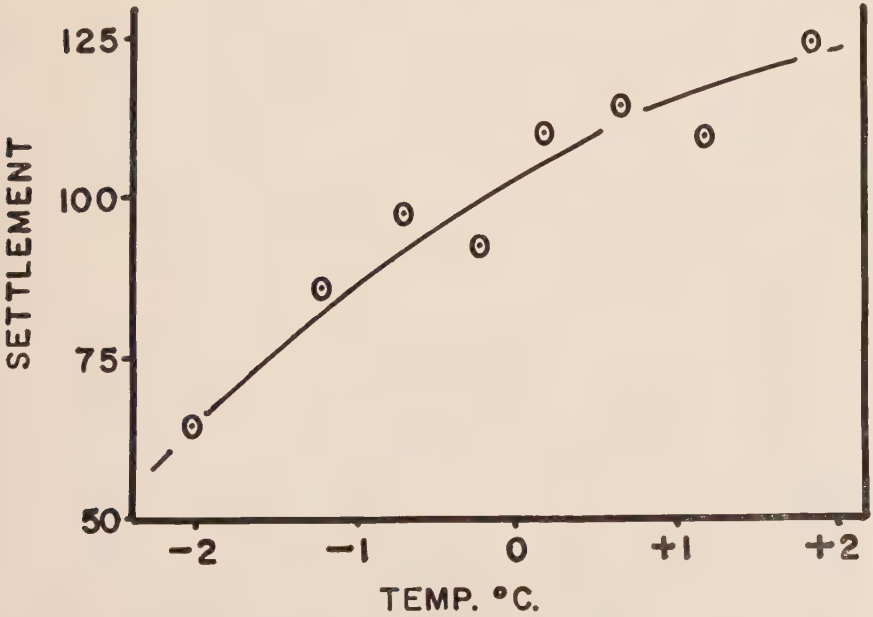

FIGURE 4. The relation of cypris settlement (cycle eliminated values) to deviation of temperature from the twelve year mean for the month.

the results shown in the second graph in Figure 3, and it will be seen that the summer peak becomes more pronounced with this treatment. The use of twelve year means tends to flatten the individual peaks which may be much more sharply defined in some years. On the other hand, in some years, one, or even two of the peaks may be almost missing. The general seasonal trend does not correlate closely with either temperature or river discharge.

The seasonal cycle was next eliminated by dividing each of the monthly long period cycle eliminated values by the twelve year mean for the corresponding month. The fluctuations of the resulting cycle-eliminated data could then be compared with deviations of temperature and river discharge for the month in question from the twelve year mean for that month. No correlation was found with river discharge, but a close positive correlation with temperature (Fig. 4). This indicates about a 13% increase in settlement per degree centigrade above mean temperature.

To show possible lunar rhythm in settlement, the original data for each month were grouped into three approximately ten day periods. The mean for each ten day period was then expressed as a percentage of the mean for the whole month. In this way both long period and seasonal cycles were eliminated. The data was then grouped according to the number of days from new moon to the mid day of the period,

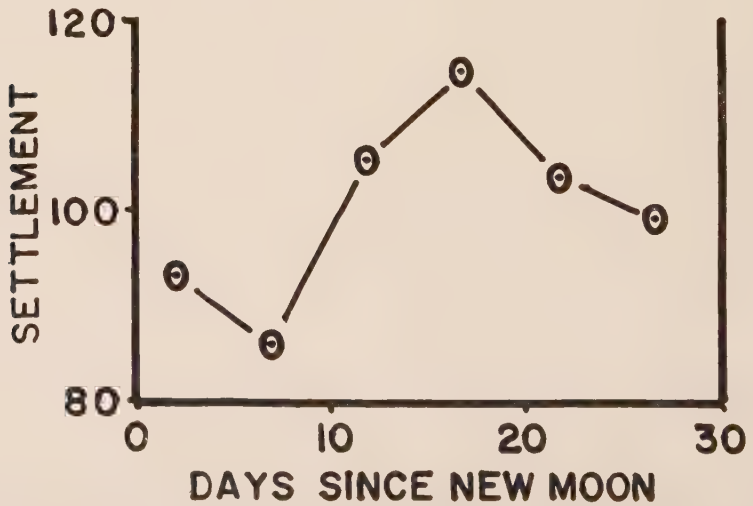

FIGURE 5. Relation of cypris settlement (expressed as the percentage of the mean value for the month) to the age of the moon.

and the results are shown in Figure 5. There is a range of about 30% and a marked maximum shortly after full moon. This cycle might reflect differences in tidal currents, but it is more probable that it is the result of a lunar rhythm in spawning.

Balanus improvisus. It is possible to study the factors affecting survival during the first month if it is assumed that there is no marked differential mortality between the species. This assumption is probably valid since *B. improvisus* comprises over 80% of all the surviving barnacles. We have assumed that the total settlement of *B. improvisus*

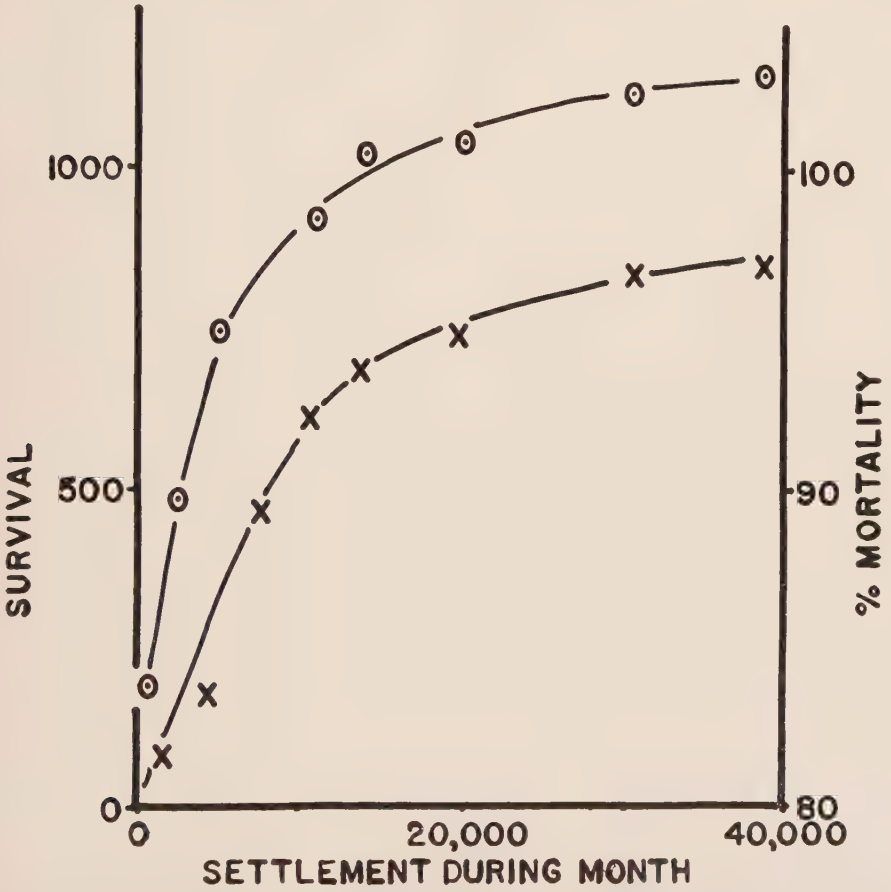

FIGURE 6. *B. improvisus.* The relation of number surviving at the end of one month (O), and of percentage mortality (X), to the total settlement of cypris during the month.

for the month is equal to the sum of the cypris counts for each day multiplied by the fraction of *B. improvisus* in the total at the end of the month. One factor which clearly has a marked influence on survival is the degree of crowding on the panels. Figure 6 shows the total at the end of a month plotted against the total settled as determined from the 24 hour panels, and also the relation of mortality to settlement. The mortality rate is about 80% on the least crowded panels and approaches 100% asymptotically. The maximum population which the panel can support seems to be about 1,100, or about two barnacles per square centimeter. As the larger barnacles, in summer, exceed 12 mm in length, this is not surprising.

Since crowding strongly influences survival, it is necessary to eliminate its effect before the influence of other factors can be studied. The monthly percentage survivals were therefore divided by a percentage survival corresponding to that density of settlement, and multiplied by 100. This gave crowding-eliminated values, which showed a marked

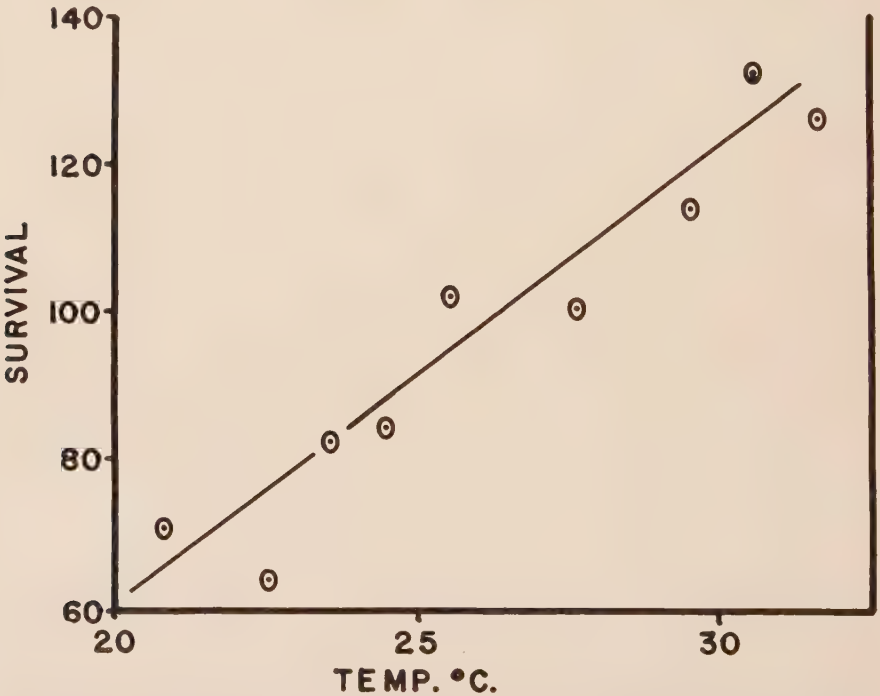

FIGURE 7. *B. improvisus*. The relation of survival on one month panels (after correcting for the effect of crowding) to temperature.

positive correlation with temperature (Fig. 7) and a negative correlation with river discharge (Fig. 8). Using the regressions from these, and monthly values of river discharge and temperature, weighted in proportion to the cypris settlement in those months, it was possible to predict the long period cycle of crowding-eliminated survival with fairly close agreement with the observed figures.

The long period cycle was eliminated as before and the 12 year means for the months were obtained with the results shown in Figure 9. As with cypris settlement, crowding-eliminated survival shows three summer peaks, the first slightly before that for settlement, and the other two about a month before. The general trend follows most closely that for temperature (Fig. 2). The seasonal cycle also was next eliminated and the residual fluctuations compared with deviations of temperature and river discharge from the twelve year means for the months concerned show a positive correlation with temperature and a negative correlation with river discharge, both significant.

For the purposes for which these panels are used it is not necessary

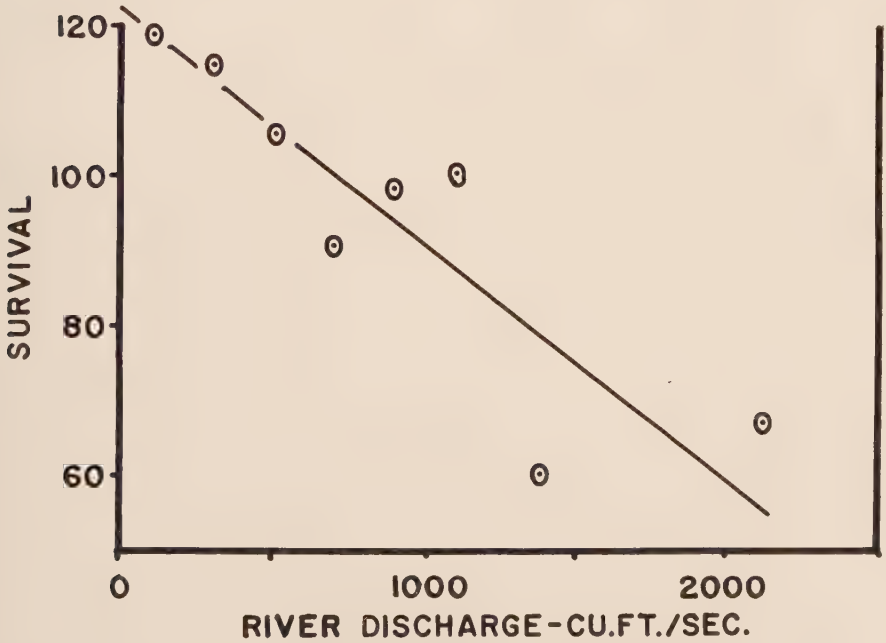

FIGURE 8. *B. improvisus*. The relation of survival on one month panels (after correcting for the effect of crowding), to river discharge.

to record sizes greater than 12 mm. Growth studies therefore have had to be restricted to the winter months of November to March when a maximum size of 12mm is rarely attained, and probably never exceeded. Fig. 10 shows the long period variation in winter growth, together with winter river discharge. There is a significant negative correlation between growth and river discharge, but none with tem-

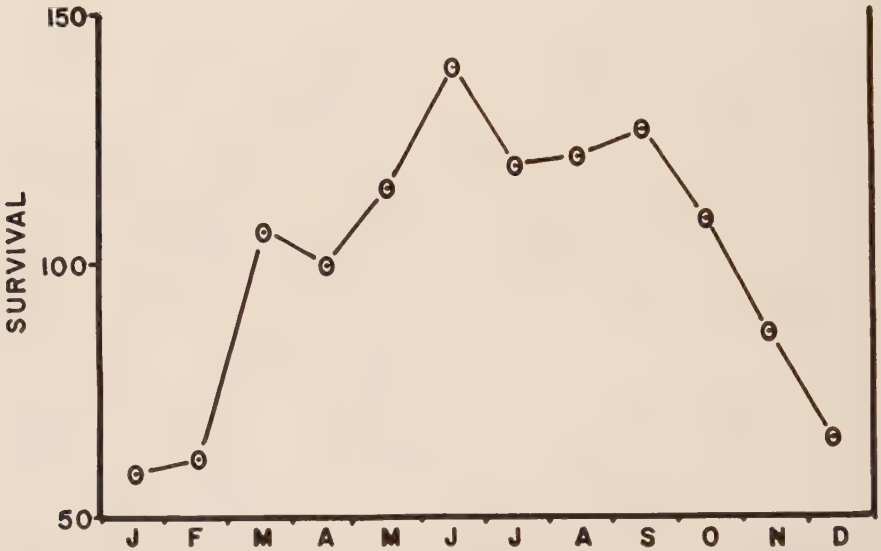

FIGURE 9. *B. improvisus.* The seasonal variation in survival on one month panels after eliminating the effects of crowding and long period cycles.

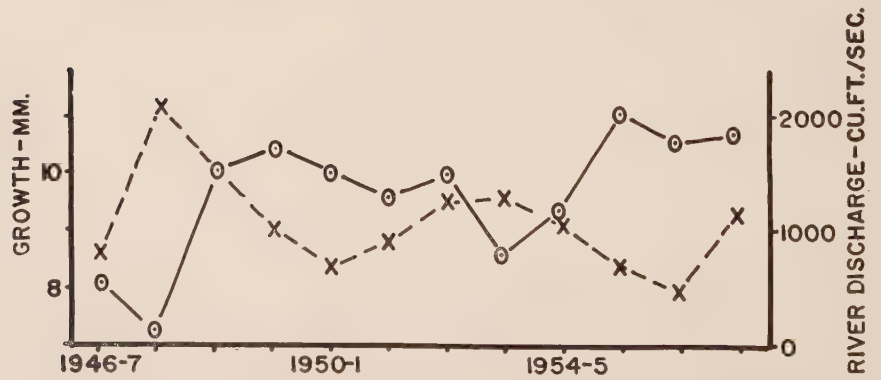

FIGURE 10. *B. improvisus.* Comparison of the long period cycle for winter growth (O) with that of winter river discharge (X).

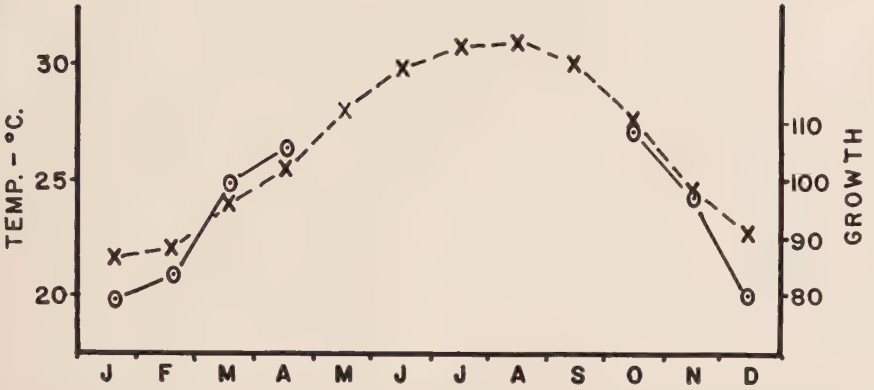

FIGURE 11. *B. improvisus*. The seasonal cycle of growth on one month panels (after elimination of the effect of long period cycles) compared with the mean seasonal cycle of temperature.

perature. Elimination of the long period cycle yields the mean seasonal cycle shown in Figure 11, and it is apparent that there is a close positive correlation with temperature. Elimination of the seasonal cycle also and comparison of the residual fluctuations with deviations of temperature and river discharge from their 12 year means for the months in question show a negative correlation with river discharge (Fig. 12), but none with temperature.

Balanus amphitrite. This species comprises 12.5% of the barnacles over the whole 12 year period, so significant analysis of its relationships cannot be carried as far as was possible in *B. improvisus*. It is not possible to determine percentage survival or the effect of crowding. The numbers surviving on the one month panels show a pronounced long-period fluctuation with a significant negative correlation with river discharge (Fig. 13), but none with temperature. After elimination of the long-period cycle, the 12 year mean seasonal cycle was determined (Fig. 14). This shows a very abrupt break between a high summer rate and a low winter rate. Between March and October there is a slight increase in rate, but no evidence of the three peaks found both in *B. improvisus* and in the attachment of cypris. The fluctuations remaining after elimination of both long period and seasonal cycles show no correlation with either temperature or river discharge.

Growth data again are limited to the winter months when values did not exceed 12 mm. The long period cycle (Fig. 15) shows a fairly steady increase throughout the period, but with no correlation with

temperature, river discharge or growth of the other species. Annual mean temperatures generally increased during the period, but this does not apply to the winter temperature; river discharge also generally decreased. The short period fluctuations, however, show no correlation with those in temperature or river discharge. Elimination of the long period cycle gives the 12 year mean seasonal cycle shown in Figure 16 in which there appears to be a positive correlation with temperature. The fluctuations remaining after elimination of the seasonal cycle also show a significant negative correlation with deviations of river discharge form the mean for the month (Fig. 17) and a small but significant positive correlation with similar deviations of temperature.

Balanus eburneus. Numbers are least adequate in this species which

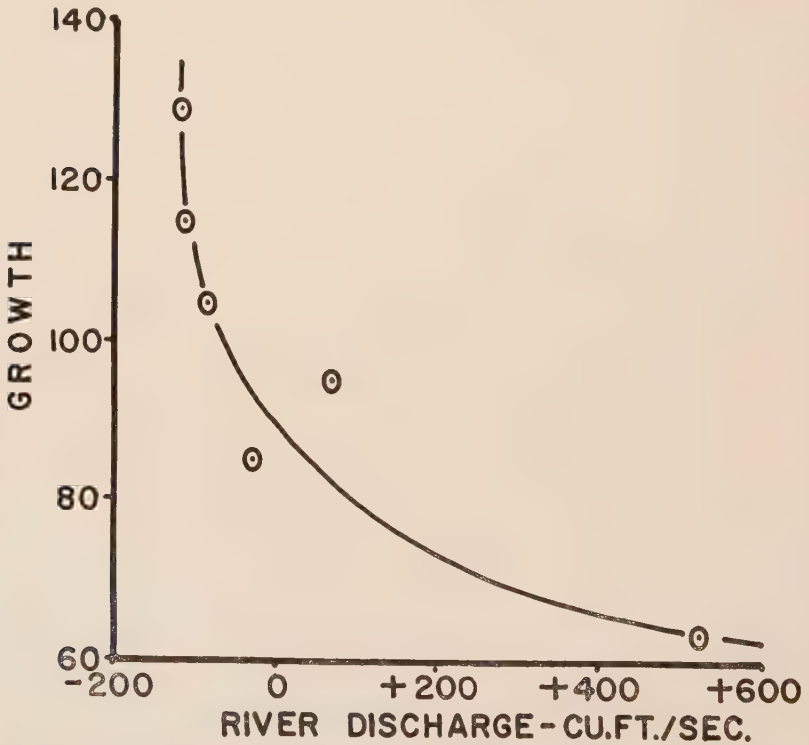

FIGURE 12. *B. improvisus*. The relation of winter growth on one month panels (after elimination of the effects of long period and seasonal cycles), to river discharge.

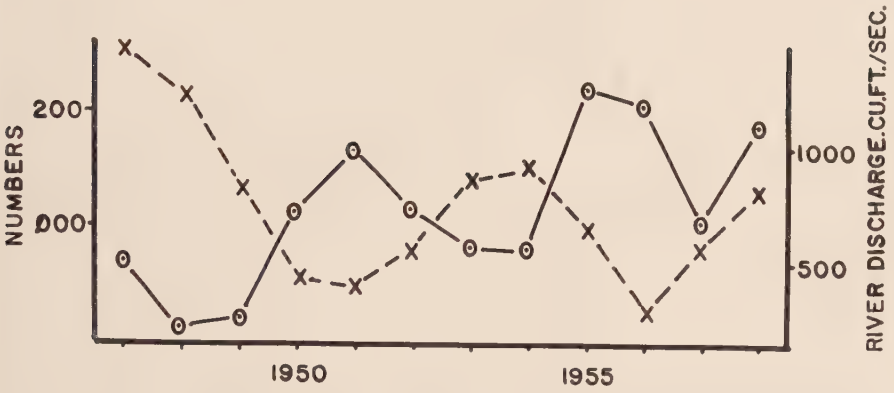

FIGURE 13. *B. amphitrite*. The long period cycle of survival on one month panels (O) compared with that of river discharge (X).

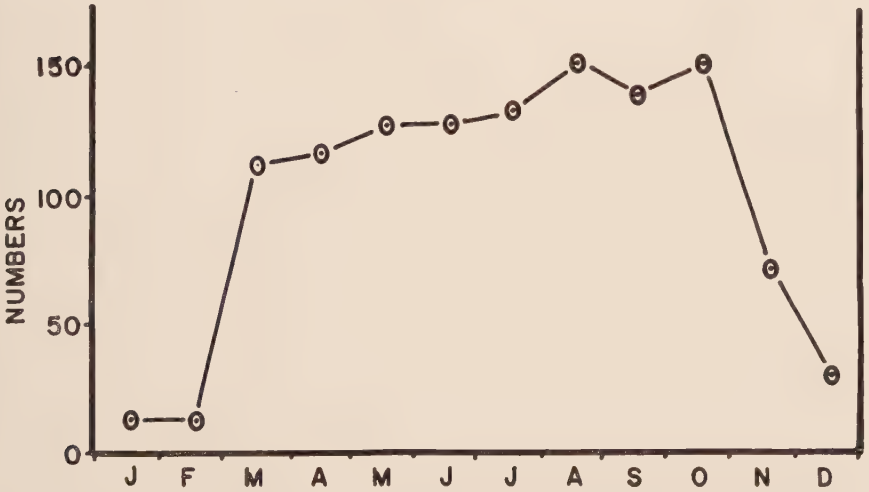

FIGURE 14. *B. amphitrite*. The seasonal cycle of survival on one month panels after elimination of the effects of long period cycles.

constituted only 6.7% of the total barnacles attached during the period. The long period cycle in numbers surviving on the one month panels show a general increase throughout the period, and a positive correlation with the cypris settlement, suggesting similar factors controlling both (Fig. 18). However, there was no correlation with river discharge, and a positive correlation only with the temperatures for the

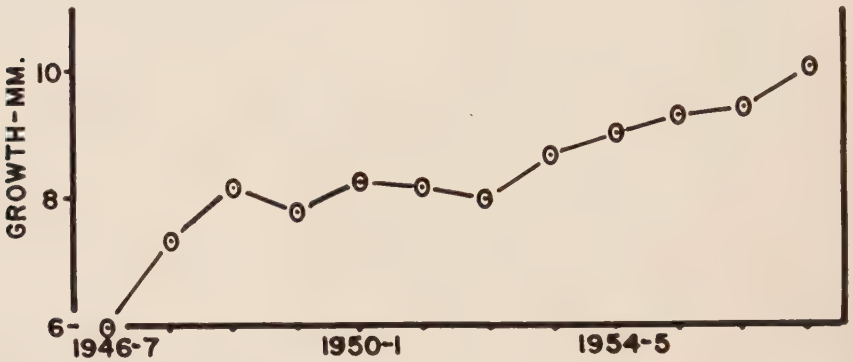

FIGURE 15. *B. amphitrite.* Long period cycle of winter growth on one month panels.

previous year. With the long period cycle eliminated, the seasonal cycle of attachment shows three peaks as in *B. improvisus,* with the autumn one by far the most pronounced (Fig. 19). The long-cycle eliminated data show a strong positive correlation with temperature (Fig. 20), and with the seasonal cycle also eliminated there is still a small but significant positive correlation with temperature, but in neither case is there any correlation with river discharge.

There were so many winter months with no settlement that all that can be said about winter growth is that it ranged from about eight to eleven mm in the first month. Summer growth was 12 mm or more, and in some cases is recorded as 15 mm.

DISCUSSION

This study has raised a number of questions, particularly with regard to growth rates and age at maturity, which are now under investigation. The discussion will therefore be limited to a few outstanding points. The three species differ considerably in geographical distribution. *B. improvisus* ranges from the Baltic and southern Norway, through northern Spain to the Mediterranean, Black Sea and Caspian. On the eastern coast of America it ranges from Canada to Patgonia. On the west coast it is recorded from California and Columbia. Apparently absent in the rest of the Pacific, it is recorded from the Red Sea but not around the African coasts outside the Mediterranean. It approaches freezing temperatures in Canada, the Baltic and Patgonia, and tolerates high summer temperatures in the Red Sea and Caribbean, so has a

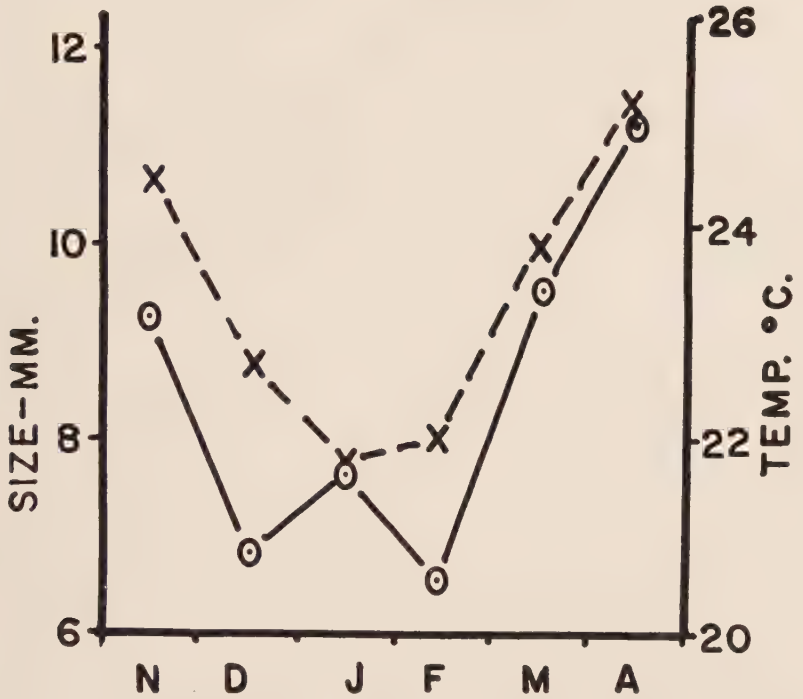

FIGURE 16. *B. amphitrite.* Winter growth on one month panels after elimination of the effects of long period cycles, and mean winter temperatures.

temperature range of over 30°C. It tolerates a wide range of salinity also, occurring from fully marine conditions to water which is completely fresh for part of the tidal cycle, or comparatively fresh at all times. Its optimum is probably at intermediate salinities (Bousfield, 1954).

Balanus amphitrite, taking all its subspecies together, has a more extensive distribution than the last species, being widespread in the Pacific. It is restricted to a slightly warmer range: present in the North Sea but absent from the Baltic, reaching north to Massachusetts but not to Canada on the east coast of America, and excluded from the colder southern part of South America but reaching Vladivostock in the Pacific. It is much less tolerant of low salinity, not normally occurring under estuarine conditions, and being absent from the Baltic, (perhaps because of low temperature rather than low salinity there), and from the Black Sea and Caspian.

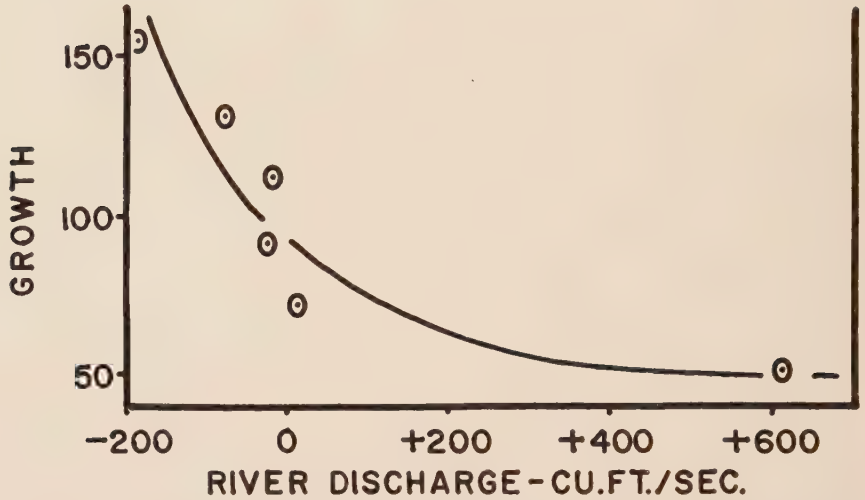

FIGURE 17. *B. amphitrite.* Relation of deviation of mean winter growth on one month panels from mean growth for the month to deviation of river discharge from mean for the month.

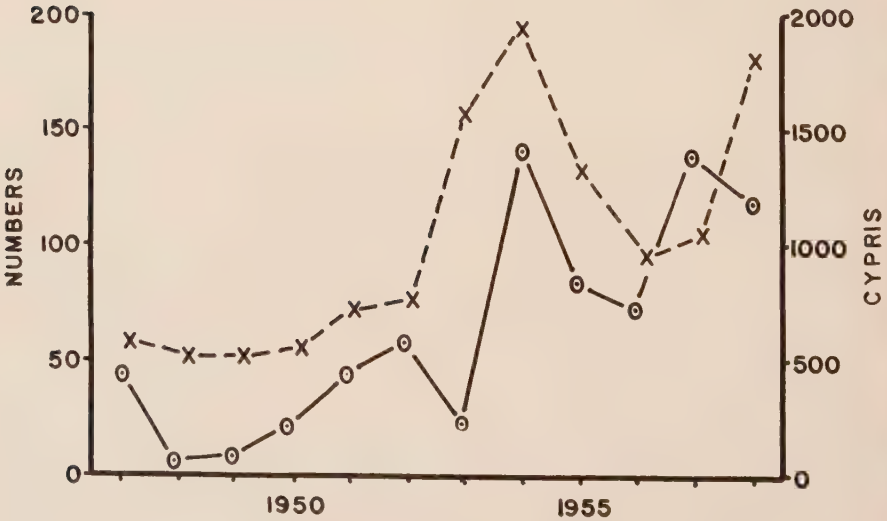

FIGURE 18. *B. eburneus.* Long period cycle of survival on one month panels (O), compared with that of cypris settlement (X).

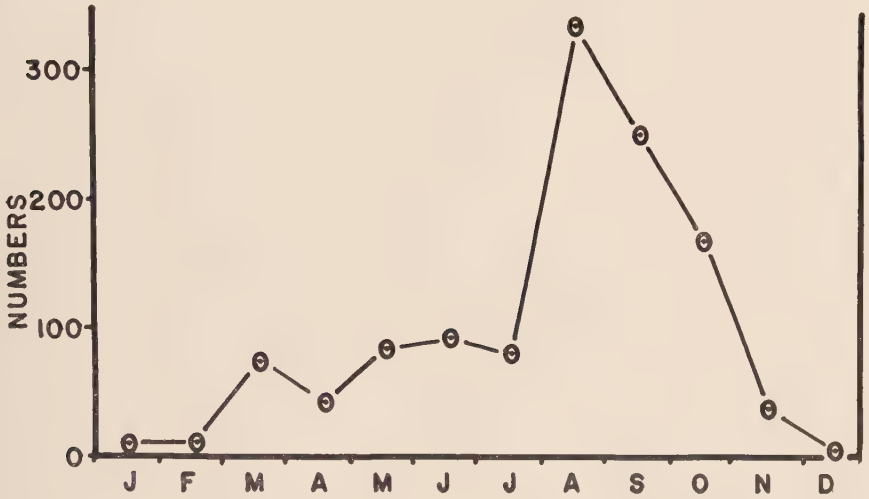

FIGURE 19. *B. eburneus*. Seasonal cycle of survival on one month panels after elimination of effects of long period cycles.

B. eburneus has a much more restricted distribution than either of the other species. On the western side of the Atlantic it ranges from Massachusetts through the Gulf of Mexico and West Indies to the Caribbean coast of South America. It apparently invaded Europe about a hundred years ago and is now found on parts of the French and Spanish coasts and in the Mediterranean, Black Sea and Caspian. It has also been recorded from Hawaii. It appears, thus, to be slightly more restricted again in temperature. On the other hand it is highly tolerant of low salinities and is recorded from regions where the water appears to be fresh for considerable periods (Fischer-Piette and Prenant, 1956). In the Miami area it penetrates further into the Miami river than do either of the other species, and it is the only one of the three that has been found in the very brackish waters of Coot Bay.

Weiss (1948) has published counts of total barnacles on one month panels, made at this same station from 1943 to 1946. The steady increase in rate of attachment during the sixteen years (Fig. 1a) parallels the growth of the local population and may well reflect the increase in docks, bulkheads, boats, etc., which provide attachment for barnacles, and so a source of larval production. If we assume such a steady increase in larval production, then cypris attachment reflects both this and a benefit from increased temperature or river discharge. Its seasonal cycle also reflects the seasonal temperature changes, and there is

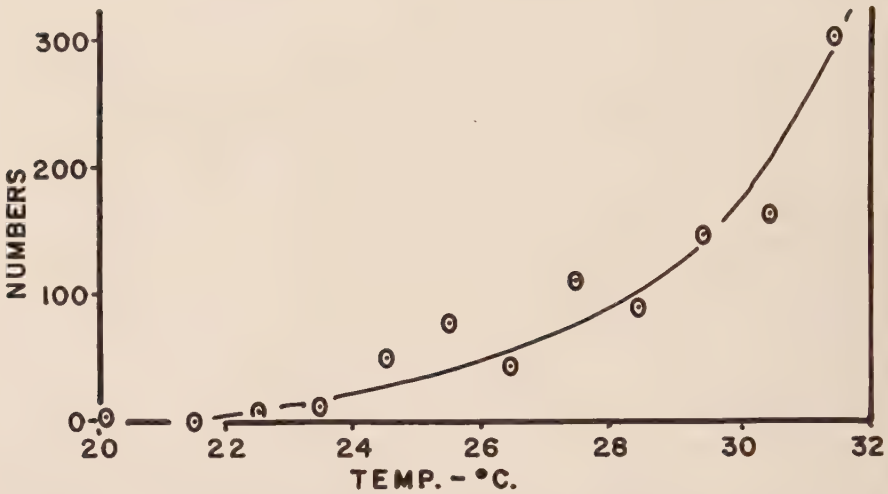

FIGURE 20. *B. eburneus.* Relation of survival on one month panels, after elimination of the effects of long period cycles, to temperature.

some dependence also on a lunar cycle. Settlement, further, shows three separate peaks in March, July and October. Since *Balanus improvisus* is the dominant species among those found on one month panels, it may be assumed that the above applies to the larvae of this species but might well be less true of the less abundant *B. amphitrite* and *B. eburneus.*

Survival of *B. improvisus* is increased by higher temperatures and decreased by crowding and high river discharge. For the other two species there are data available on numbers surviving on the one month panels, but not on percentage survival during that month. In *B. amphitrite,* survival shows a negative correlation with river discharge, but none with temperature while in *B. eburneus* there is a positive correlation with temperature, but none with river discharge. From their distribution in other parts of the world it is known that *B. amphitrite* is not tolerant of low salinity, while the other two species are very tolerant, with *B. eburneus* perhaps the more so of the two. Geographic distribution offers information on relative tolerance of low temperatures, but does not distinguish between their distributions at the warm end of their range, so there is no comparison with the absence of temperature sensitivity in *B. amphitrite* in the present observations.

The seasonal survival curve for *B. improvisus* shows three peaks similar to those found for cypris settlement, but with the survival peaks

preceding the settlement peaks. The seasonal survival cycle of *B. eburneus* shows three similar peaks, but that for *B. amphitrite* does not show them. The repetition of these three peaks in different species, in different types of observation and in data obtained from two different sets of test panels (the 24-hour and the one month panels) adds support to the belief that they are really significant. The absence of correlation with any obvious environmental factor suggests that they are the result of an internal cycle in the barnacles, and the most probable cycle seems to be three successive spawnings. There are two possibilities: individuals may spawn three times during the year, or there may be three successive generations which settle, mature and spawn, and may either die or continue to spawn a second time. The suggestion of successive generations would call for a very rapid rate of growth and maturation, but this is not impossible. Weiss (1948) has already suggested such a possibility. Grave (1933) states that *B. eburneus* reaches sexual maturity at two months at Woods Hole, and Bousfield (1954) gives three months for *B. improvisus* in Canada, both at considerably lower temperatures than at Miami. Costlow and Bookhout (1957) give a larval life for *B. eburneus* in North Carolina of 7-13 days as nauplii and not more than three days as cypris. Grave gives 7-10 days for the total planktonic life of this species at Woods Hole. D. Tabb (personal communication) has found *B. eburneus* in Coot Bay, south of Miami, not more than two months old and carrying nauplii nearly ready to release. This was in winter. An approximately three month cycle in the Miami area is therefore not improbable, but further tests, now in progress, will be required to verify this. Coe (1932) found that *B. tintinnabulum* passed through two generations in a year in California.

Growth data call for further observation. Growths in one month over 12 mm were nearly always recorded at this value, and furthermore, crowding in the summer months probably seriously affects growth as it does survival. However, there are some possible comparisons. One month growth of *B. eburneus* at Miami drops below 10 mm in only two of the winter months. At Woods Hole, summer growth is slightly below this figure (Grave, 1933), and the maximum size, attained at about one year, is about 20 mm. This is considerably exceeded in Miami. Bishop *et al.* (1957) refer to 18 mm individuals from the French coast as being "of very large size." At Beaufort, N. Carolina, it is recorded as growing to 12 mm in one month, and 20 mm in five

months (McDougall, 1943). This is comparable with the Miami results. *B. amphitrite* in Hawaii reaches 15 mm in 28 days and 24 mm in 342 days (Edmondson and Ingram, 1939), and at Pearl Harbor also it reaches 24 mm in one year (Edmondson, 1944). It first spawns at 12-15 mm. These figures again seem comparable with Miami values.

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CELLULOLYTIC ACTIVITY IN LIGNICOLOUS MARINE ASCOMYCETES[1, 2]

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ABSTRACT

Cellulolytic activity, determined by the Nelson-Somogyi method, has been demonstrated in *Lulworthia floridana* Meyers, *Torpedospora radiata* Meyers, *Ceriosporopsis halima* Linder, *Lignincola laevis* Höhnk, *Peritrichospora integra* Linder, and *Arenariomyces salinus* Meyers. Cell free filtrates of these species acting on cellulose and powdered balsa wood substrates, under designated incubation conditions, produced approximately 0.075-0.150 mg. reducing sugar (RS)/ml., with maximum RS production at less than 0.3 mg./ml. Cellulolytic activity of a given filtrate varies considerably with the type and amount of substrate and the conditions of incubation. The amount of effective cellulases produced by these fungi on wood in the sea is not determinable. However, previous *a priori* evidence noting the presence of a cellulose degradating mechanism in species of lignicolous marine fungi has been substantiated.

INTRODUCTION

The characteristics and degradative processes of those fungi which attack terrestrial woody plants and cellulosic materials have received considerable study. Among the more recent discussions of this subject are the works by Walseth (1948), Jennison *et al.* (1952), Wise and Jahn (1952), and Cowling (1958). Although a large number of such fungi participate in diverse activities culminating in the eventual destruction of the wood substrate, it is commonly believed (Cartwright and Findlay, 1950) that only certain Basidiomycetes and a few Ascomycetes can decompose the ligno-cellulose tissue of wood.

There has been considerable interest in possible cellulolytic activity of lignicolous fungi in the marine environment. The presence of a large and varied flora of ascomycetous and deuteromycetous species on wood submerged in the sea has been demonstrated repeatedly (Johnson and Meyers, 1957). Much *a priori* evidence has accumulated concerning the role of these marine fungal species in the destruction of wood (Meyers and Reynolds, 1957; Reynolds and Meyers, 1957). This includes sloughing or softening of the wood surface, penetration and complete vegetative and reproductive infestation of submerged wood panels, and a growth-wise affinity for wood and wood products in pure culture. Furthermore, recent studies (Kohlmeyer, 1958)

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[2]Contribution No. 245 from The Marine Laboratory, University of Miami.

suggest ecological and nutritional relationships between species of marine fungi and wood boring animals.

Heretofore, analytical determinations of cellulolytic activity in lignicolous marine fungi have been lacking, although indirect evidence for enzymatic activity has been noted (Barghoorn and Linder, 1944). Such determinations are essential to a thorough understanding of the dynamics of these fungal species, and their contribution to marine biology. In this present work, preliminary enzymatic studies of selected marine ascomycetous species are reported, using an increase in reducing sugars as an index of the hydrolysis of cellulose and cellulosic materials.

The authors wish to acknowledge the interest and invaluable suggestions of the following individuals: Dr. E. T. Reese, Quartermaster Research and Development Center, U.S. Army, Natick, Massachusetts; Dr. K. W. King, Virginia Agricultural Experiment Station, Virginia Polytechnic Institute, Blacksburg, Virginia; Dr. D. R. Whitaker, National Research Laboratories, Ottawa, Canada; Dr. P. Kooiman, Technical University, Delft, Holland; Dr. E. B. Cowling, Forest Products Laboratory, U. S. Department of Agriculture, Madison, Wisconsin. The opinions expressed in this paper, however, are those of the authors. Mr. Joe Levi of The Marine Laboratory assisted ably in the performance of numerous technical aspects.

Materials and Methods

Stock cultures. The ascomycetous species used included: *Lulworthia floridana* Meyers, *Torpedospora radiata* Meyers, *Ceriosporopsis halima* Linder, *Lignincola laevis* Höhnk, *Peritrichospora integra* Linder, and *Arenariomyces salinus* Meyers. Stock cultures of these fungi are maintained in the mycological collection of The Marine Laboratory on a sea water agar medium of 0.1 per cent yeast extract (Difco) and 1.0 per cent glucose. The majority of tests were run with *L. floridana* and *T. radiata.* These two species rapidly attack submerged wood and exhibit excellent vegetative and reproductive development in culture on various nutrient sea water media. Sporulation on such cellulosic materials as powdered cellulose and balsa wood slips in 0.1 per cent yeast extract sea water broth is common.

Growth conditions. The fungi were grown in 250 ml Erlenmeyer flasks containing 40-50 ml of 0.1 per cent yeast extract sea water broth. Inocula consisted of small mycelial and agar pieces or conidial suspensions from stock cultures. The sea water for tests and growth studies

was taken from Biscayne Bay, Florida, filtered through an M-grade sintered glass funnel, and stored in carboys in the dark. Both stationary and shake cultures were used, the latter on an intermittent reciprocating apparatus constructed in the laboratory.

The cellulosic material used for the growth and enzymatic studies included: Whatman ashless cellulose powder, Standard Grade for chromatography; Alphacel (Nutritional Biochemicals Corp.); Rayocord-X (F), a southern pine sulfite pulp (Rayonier, Inc., New York City); and balsa wood (International Balsa Corp., New York City). The Rayocord and balsa wood were ground through a Wiley mill to pass a 40 mesh sieve. In the growth tests, these materials were supplied at 1.0 per cent concentration.

The soluble cellulose derivative, used for comparative purposes, was Sodium Carboxymethylcellulose, CMC-70 High, with a DS of 0.65-0.85 (Hercules Powder Co.).

Balsa wood slips also were used for the development of the fungi. In subsequent sections of this paper, reference to the growth of these fungi on balsa wood indicates specifically that on the intact slips. The latter were cut to remain slanted in the flasks, with the lower portion of the wood immersed in the liquid medium. In these cultures, vegetative and reproductive development of the various species occurred on the submerged and aerial wood surfaces, with slight mycelial growth within the liquid itself. In most of the shake flasks with powdered cellulose materials, the fungal growth was in compact pellets, or aggregates, common to such cultures. In *L. floridana* and *T. radiata,* perithecial development occurred in the pellets as well as along the sides of the flask where material had been dispersed by the shaking process.

Preparation for analysis. The following procedure was used to prepare the material for the determination of its cellulolytic activity:

a. The entire liquid portion from a given culture was filtered successively through a No. 10 and a No. 01 Selas porcelain crucible filter. The latter filter is rated as having a maximum pore radius of 3 microns. In many of the cultures with balsa wood slips the entire fungal permeated wood and broth were mixed thoroughly in an Osterizer blendor for 5 minutes, and the liquid from this total macerated wood pulp sample filtered as above.

b. Five ml samples of the cell free filtrate were placed in 125 ml Erlenmeyer flasks with either, (a) 5 ml of isotonic phosphate buffer and 200 mg of powdered cellulose, balsa, or Rayocord, or (b) 5 ml of 1.0 per cent CMC prepared in isotonic phosphate buffer. This dilu-

tion brought the final CMC concentration down to 0.5 per cent, the phosphate buffer to 1/30 M concentration, and the sea water to half strength. Toluene was added, the flasks stoppered and the material incubated under the designated conditions.

c. The liquid from flasks with insoluble cellulosic materials was filtered through a No. 01 Selas crucible filter prior to the determination. All samples were treated identically and diluted to standard volume. Tests were run in duplicate on 1 ml aliquots, and calculations of the mg reducing sugar/ml or mg RS/ml were on this basis.

d. Determinations of the reducing sugars were made on the full strength fungal filtrate from each culture to obtain the initial RS value.

Test conditions. Sorensen's phosphate buffer, made isotonic with sea water by the addition of NaCl, was used. Incubations were run at pH 5.6-5.8, at temperatures of 25°, 37° and 60°C, with the majority of the tests at 37°C. For comparative purposes, selected solutions were run at all three temperatures.

The time of incubation of the cellulolytic solutions on the "natural" cellulosic substrates was varied from 24 to 120 hours. The initial 72 hour period proved to be of most interest. On the CMC substrate, incubation periods of ½, 1 and 2 hours were selected.

Toluene was used as a preservative in these tests and in the cell free filtrates stored at refrigerator temperature.

Cellulolytic solutions, designated "CS," were derived from fungal cultures on various cellulosic materials. In the section on results, following the CS number, there is noted the particular substrate on which the fungus was grown and the total growth period recorded in days.

Determination of reducing sugars. Total reducing sugars were determined by the Nelson-Somogyi method (Somogyi, 1952), with a range of 0.020 to 0.500 mg glucose/ml. Colorimetric measurements were made with a Bausch and Lomb Spectronic 20 Colorimeter, set at a wavelength of 500 millimicrons. Optical density readings were converted into milligrams from a calibrated graph, based on prepared standard glucose solutions. The graph is in excellent accord with Beer's Law.

The activity of the cell free fungal filtrates has been expressed in terms of reducing sugars (RS), rather than glucose itself. It has been noted (Halliwell, 1957) that many copper reducing compounds, other than glucose, may be produced by the action of the fungal enzymatic preparations on cellulosic materials or on cellulose in a complex, such

as in wood. The terms "RS production" and "cellulolytic activity" are used interchangeably, and refer specifically to the action of the cell free crude fungal filtrate on designated cellulosic materials under certain incubation conditions. In all procedures calling for insoluble cellulosic materials as the enzymatic substrate, 200 mg amounts were used.

In these tests, an increase in copper reduction above that determined for the particular fungal extract is interpreted as indicating cellulolytic activity, and is expressed as mg RS/ml. Corrections are made for the reducing values, usually less than 0.010 mg RS/ml, for the CMC solution and for the 200 mg samples of powdered cellulose and balsa.

Results

Lulworthia floridana. A filtrate from a 43 days' balsa wood culture of this fungus was incubated at 25° and 37°C for 216 hours on cellulose. This cell free enzymatic filtrate was prepared from the combined extract of the fungal permeated wood slip and the culture liquid. The results are summarized and plotted in Figure 1.

At 216 hours incubation, the 25° sample gave 0.115 mg RS/ml and

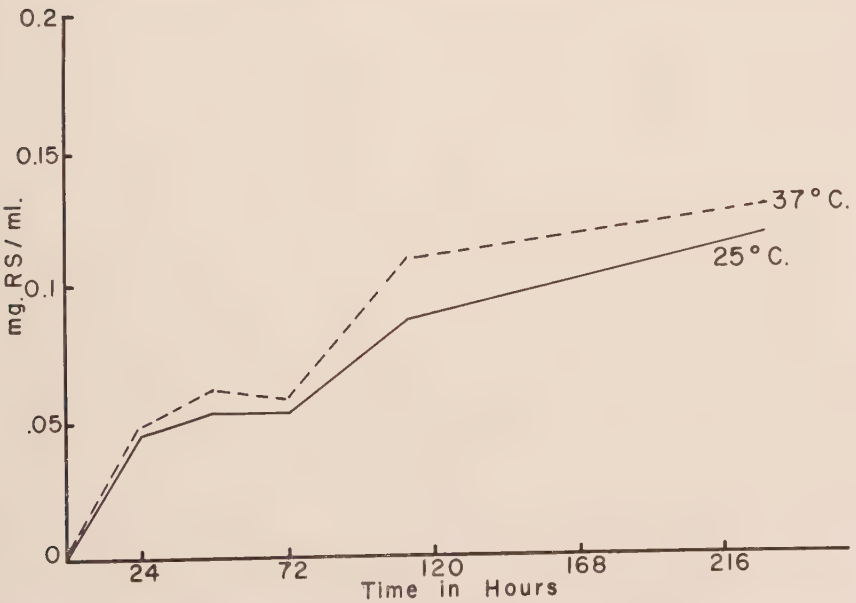

Figure 1. Activity of a cell free filtrate of *L. floridana* on powdered cellulose at 25° and 37° C.

the 37° sample, 0.125 mg RS/ml. Throughout the 216 hours, the amount of reducing sugars produced at the two temperatures was nearly the same, although slightly greater at 37°C. Some of the same enzymatic preparation incubated on balsa for 216 hours exhibited 0.118 mg RS/ml at 25° and 0.136 mg RS/ml at 37°C.

Other cultures of *L. floridana,* grown on balsa wood for various periods, from 46 to 117 days, produced 0.040-0.065 mg RS/ml upon incubation of the cell free filtrate with cellulose at 25°C for 24 hours. One enzymatic preparation (CS-32, on balsa, 77 days), gave 0.083 mg RS/ml from 200 mg balsa in 24 hours at 37°C, 0.065 mg RS/ml from a similar amount of cellulose under the same incubation conditions, and 0.075 mg RS/ml from CMC at 37°C for ½ hour.

A preliminary experiment on the effect of pH on enzymatic activity of a cellulolytic solution of this species (CS-102, on balsa, 102 days), incubated with cellulose at 25°C, is summarized in Table 1.

TABLE 1

EFFECT OF PH ON ENZYMATIC ACTIVITY IN *L. floridana*

pH	*mg RS/ml*	
	96 hrs.	168 hrs.
5.2	0.058	0.064
5.8	0.056	0.076
6.4	0.056	0.064
6.8	0.046	0.061
7.0	0.048	0.050

Differences in pH from 5.2 to 6.4 did not affect the amount of RS. Above pH 6.5, a precipitate was noted in the flask containing the mixture of cellulolytic solution and cellulose substrate. The amount of reducing sugars produced was less than that recorded in the lower pH range. The precipitation may have been due to the action of the higher pH on the PO_4 radical of the buffer.

Another filtrate of the fungus (CS-103, on balsa, 117 days), was run for 48 hours at 25°C on cellulose, at several pH levels. At pH 5.8, 0.048 mg RS/ml were obtained, while at pH 6.4 and 7.0, the RS production was 0.051 and 0.063 mg respectively. The results of this test, in which apparently greater enzymatic activity occurred in the neutral range, differs from that noted earlier where more RS production occurred in the acid range.

Torpedospora radiata. Filtrates taken from cultures of this species on

different carbohydrate substrates exhibited dissimilar degrees of activity. In Figure 2, cell free extracts from the following three cultures were incubated with 200 mg cellulose for 96 hours at 25° and 37°C. (a) CS-1, on Whatman cellulose, 146 days, (b) CS-3, on balsa wood, 168 days, and (c) CS-7, on Alphacel, 155 days.

In all three solutions, cellulolytic activity was higher at 37°C. The greatest increase in RS occurred during the first 24 hour period. CS-3 was prepared from the culture liquid itself, without grinding the balsa wood slip. This may account for the rather low yields of RS as compared with CS-30 (Figure 3), in which the total wood and culture liquid fraction was used. Preparations of CS-3 on cellulose at 25°C produced 0.044 mg RS/ml in 24 hours, while filtrates on Rayocord under identical incubation conditions yielded 0.081 mg RS/ml. CS-7 showed essentially equivalent activity both on cellulose and on balsa at 25°C for 24 hours.

The activity of cell free filtrates on balsa compares favorably with that on cellulose. Three cellulolytic solutions of *T. radiata* were tested — (a) CS-4, on Alphacel, 161 days, (b) CS-7, on Alphacel, 155 days, and (c) CS-30, on balsa wood, 63 days. In the latter prepara-

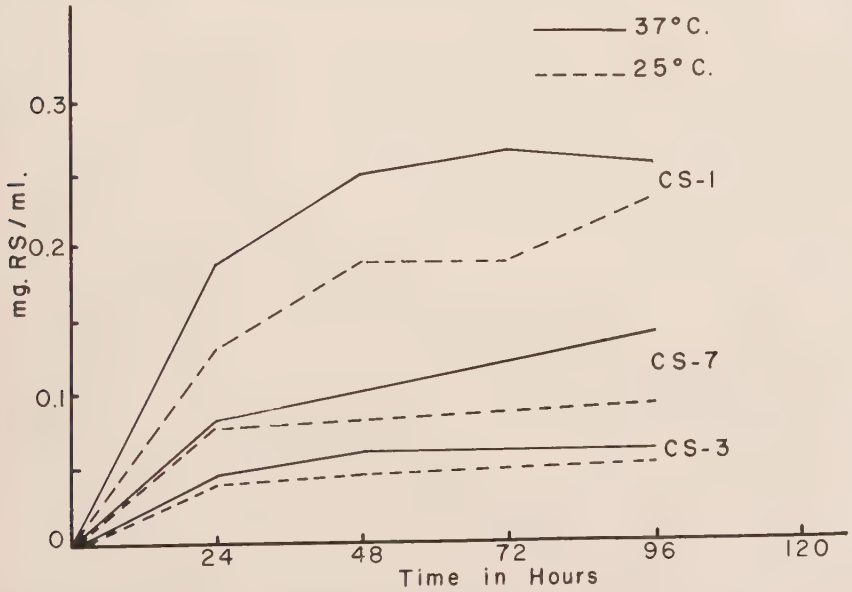

FIGURE 2. Activity of three cellulolytic solutions of *T. radiata* on powdered cellulose at 25° and 37° C.

tion, the fungal permeated wood and culture liquid were combined, and this total cell free filtrate tested. Results are noted in Figure 3.

While the growth period of 63 days on balsa wood for CS-30 equals the activity of cultures grown on Alphacel for 155-161 days, it should not be inferred that balsa wood cultures are more active than cellulose powder cultures of the same age. It is possible that a test of CS-4 and CS-7 after 63 days growth would have revealed the same amount of activity recorded after 155 and 161 days.

The activity of CS-4 was tested further on cellulose at various temperatures for periods of 24, 48 and 120 hours. The results are given in Table 2.

TABLE 2

EFFECT OF TEMPERATURE ON ENZYMATIC ACTIVITY IN *T. radiata*

Hours	*mg RS/ml*		
	25° C	37° C	60° C
24	0.078	0.092	0.100
48	0.104	0.110	0.104
120	0.130	—	0.112

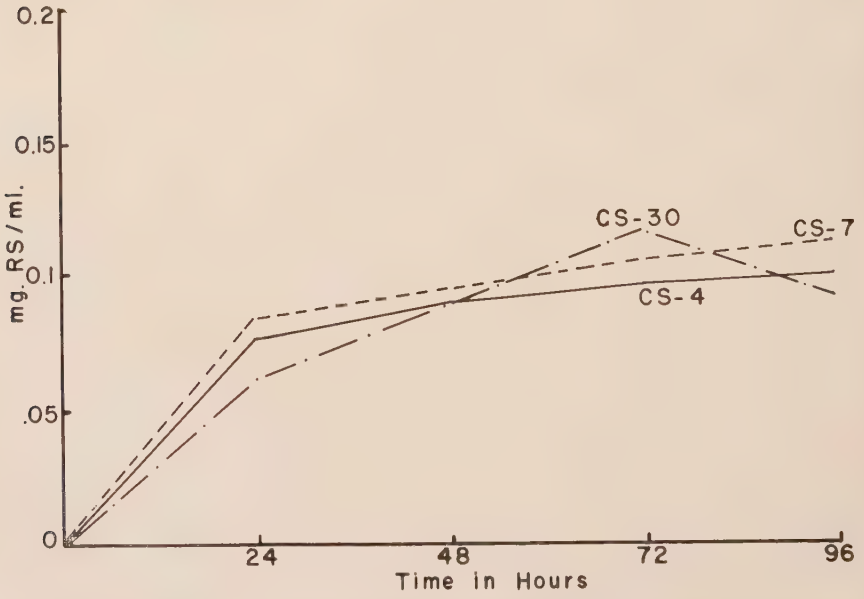

FIGURE 3. Activity of three cellulolytic solutions of *T. radiata* on powdered balsa wood. CS-7 and CS-4 at 25° C. CS-30 at 37° C.

At all three temperatures, the greatest comparative rate of RS production occurred in the first 48 hour period. In the initial 24 hours of incubation, activity was highest at 60°C, although at 120 hours, the maximum amount of reducing sugars was noted in the 25°C sample. At 37° and at 60°C, the initial 24 hours of incubation contributed the bulk of RS, while at 25°C, the lower enzymatic activity continued over a longer incubation period.

RS production showed a positive correlation with the different amounts of cellulose substrate used. Following incubation at 37°C for 24 hours, a cellulolytic solution of *T. radiata* (CS-26, on Whatman cellulose, 102 days) gave 0.040 mg RS/ml from 25 mg cellulose, 0.074 mg RS/ml from 100 mg cellulose, and 0.097 mg RS/ml from 200 mg cellulose.

Cell free filtrates from three cultures of this fungus, all growing on balsa wood for 55 days, were compared. Two of the extracts were obtained from the total homogenate of the fungal infested wood and culture liquid. The remaining preparation came from the culture liquid alone. The former two filtrates exhibited approximately twice as much activity as did the filtrate from the culture liquid itself. In these tests where the complete balsa wood and culture liquid fraction was utilized, 0.102 and 0.116 mg RS/ml were produced from 200 mg cellulose in 96 hours at 37°C, while 0.066 mg RS/ml occurred where only the culture liquid component was used.

Tests showed that activity on CMC also varied between filtrates of cultures grown on different substrates as well as on the same substrate. CS-58 was taken from a culture of *T. radiata* on Whatman cellulose for 104 days, while CS-57 was derived from a culture grown on Rayocord for 124 days. The results on CMC for a 2 hour period at 37°C are plotted in Figure 4.

The difference in activity between CS-57 and CS-58 may be attributed to the dissimilar cellulosic substrates, although excellent mycelial development occurred in both the Whatman cellulose and Rayocord culture vessels. Possibly, the dissimilar behavior of the enzymatic preparations is correlated with differences in reproductive development.

Other filtrates of the fungus were incubated with 1.0 per cent CMC for 1 hour at 37° and 60°C. These results are recorded in Table 3.

Incubation of preparations of CS-26 on 2.0 per cent CMC at 37°C for a 1 hour period yielded 0.239 mg RS/ml, as compared with the 0.197 mg RS/ml on 1.0 per cent CMC under similar incubation conditions.

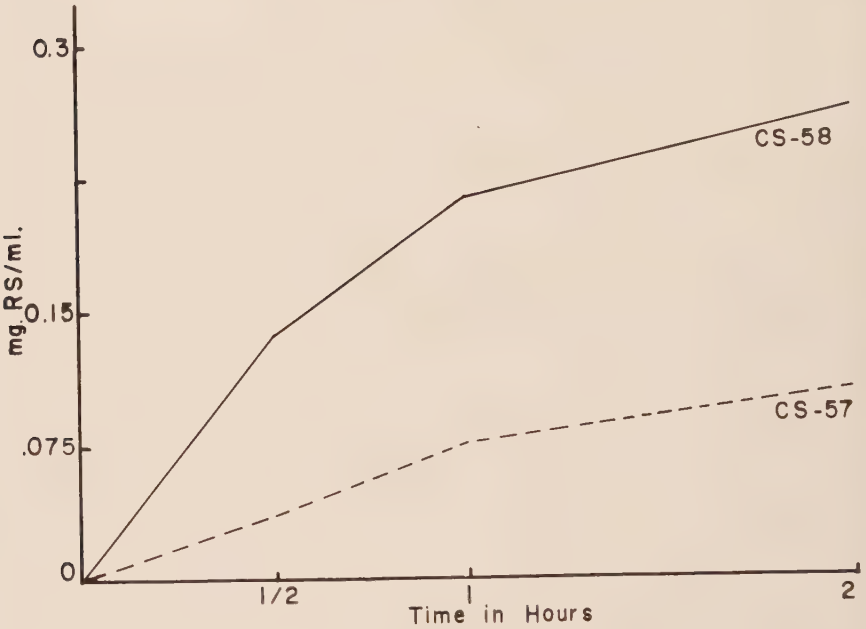

FIGURE 4. Activity of two cellulolytic solutions of *T. radiata* (CS-57, CS-58) on 1.0 per cent CMC at 37° C.

Other ascomycetous genera. Preliminary results of tests with *Ceriosporopsis halima, Arenariomyces salinus, Lignincola laevis,* and *Peritrichospora integra* are given in Figure 5. The cellulolytic solutions of all four organisms were obtained from cultures grown on balsa wood, 71 to 102 days.

Activity on CMC varied only slightly between genera, from 0.099 mg to a maximum of 0.144 mg RS/ml for *C. halima.* RS production was higher on the cellulose substrate than on balsa, except for *L. laevis,* where a greater amount of reducing sugars was produced from balsa. Activity of *P. integra* on cellulose, 0.125 mg RS/ml, was es-

TABLE 3
ACTIVITY ON CMC (1.0%) FOR 1 HOUR

	mg RS/ml	
	37° C	60° C
CS-4	0.104	0.190
CS-7	—	0.220
CS-26	0.197	0.120

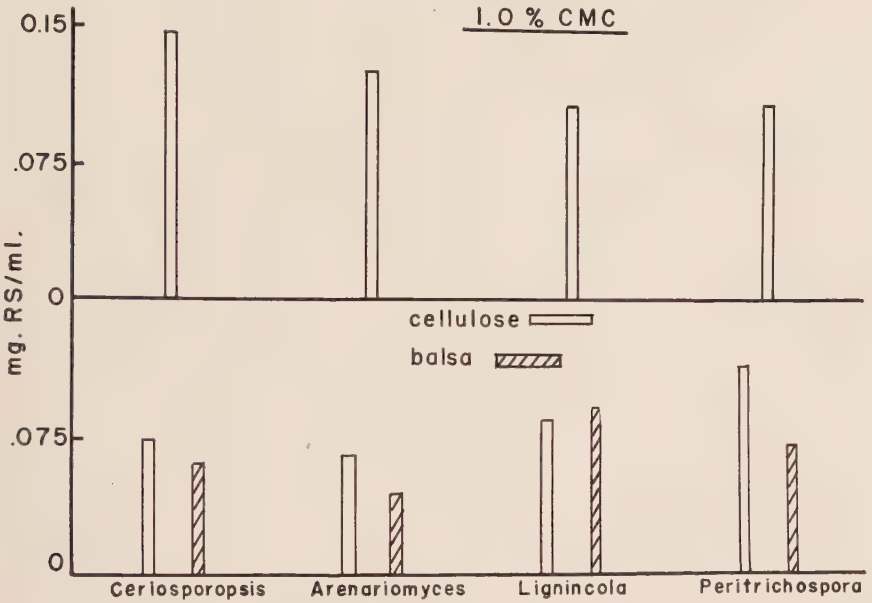

FIGURE 5. RS production by four ascomycetous genera on powdered balsa wood and cellulose at 37° C for 24 hours. Upper section shows activity on 1.0 per cent CMC at 37° C for ½ hour.

pecially high. Other tests with this species show similarly high enzymatic activity on insoluble cellulosic materials.

DISCUSSION

The results reported in this paper support the evidence from previous extensive field and laboratory studies (Reynolds and Meyers, 1957) *i.e.*, that this group of marine microorganisms possesses enzymatic mechanisms capable of degrading cellulose and wood cellulose complexes. The vigorous fungal infestation of wood in pure culture and in the marine environment suggests that a greater amount of cellulolytic activity occurs than has been detected in these enzymatic tests. In the latter, using cellulose and balsa wood as substrates, the maximum RS production was less than 0.3 mg/ml, with the average about 0.075-0.150 mg RS/ml.

This preliminary paper is not intended to give a complete qualitative analysis of the many, poorly defined, physical, chemical and nutritional factors that conceivably could affect cellulolytic activity in these species. Even less is known about the quantitative relationships

of these determinants. The difficulty of evaluating the dynamics of *in vitro* experiments in terms of the fungal processes on wood in the sea is recognized. Nevertheless, a consideration of this evaluation may be appropriate here.

Under natural conditions of attack, staling compounds and the end products of enzymatic activity, more or less, are removed from the infested wood by the leaching and abrasive action of the sea water. The continual invasion of fresh, unaffected, substrate areas by the elongating fungal hyphae provides an effective environment for enzymatic production. Thus, in the marine habitat, the biochemical processes of the fungi function more effectively than in a restricted culture vessel. Moreover, in artificial culture, the depletion of essential metabolites may limit the growth of the organism and its enzymatic activity.

Other factors also invalidate a direct comparison of *in vitro* and field studies. The enzymatic activity measured by the reducing sugar method determines only the relative amounts of the enzyme(s) functioning under our specific experimental conditions, and not the velocity of the reaction. Due to the unknown amount of retention of enzymes on the residual substrate, it is difficult to estimate the quality and quantity of the various enzymes in the fungal filtrates. In balsa wood cultures, such retention may be especially significant.

In the present cultural studies, the cellulosic and nutritional substrates used are believed to be types of materials represented in the sea water environment of these organisms. It is reasonable to consider that the activities of these fungi, on powdered cellulose and intact balsa wood in sea water cultures, with only small amounts of yeast extract added, more nearly simulate the typical degradative processes of these lignicolous fungi than they would if high concentrations of readily available, soluble carbohydrates, such as glucose, and of proteinaceous compounds were supplied. The use of 0.1 per cent yeast extract as a total nitrogen and vitamin supplement is not excessive by any means. For it has been noted (Barghoorn and Linder, 1944) that these fungi under natural conditions very commonly become established on material covered by surface growths of various benthonic organisms. These latter produce, upon decomposition, a readily available supply of organic nitrogen and other growth stimulating material.

Cellulose and wood substrates have been used as substrates in the measurements of enzymatic activity of the cell free fungal filtrates. The tests with CMC are largely comparative, since it has been shown (Siu,

1951) that activity on soluble substituted cellulose derivatives is common for both cellulolytic and non-cellulolytic organisms, while the degradation of the insoluble celluloses is characteristic only of the former group.

A direct comparison of the cellulolytic activity of these marine species with that of terrestrial fungi is difficult, and of doubtful value. The physiological cultural characteristics of our isolates are different from those of non-marine species. Similarly, fungal attack upon wood submerged in the sea differs from the infestation of cellulosic material in aerial and soil habitats. In the former instance, the wood is in a saturated condition, and represents a different physical and nutritional complex than such material exposed in the terrestrial environment. Water temperature and other hydrographic factors also are important determinants in assessing the activity of these marine species and their infestation of wood. In northern and boreal localities, wood panels have been exposed for as long as 1 to 2 months before fungal attack could be detected, while in warmer oceanic areas, infestation of wood may occur within several days to one week following submergence (Meyers and Reynolds, 1958).

More intensive studies are in progress at this laboratory on these and other lignicolous marine ascomycetous and deuteromycetous species. This work includes measurements of the amount of glucose in the total RS fraction, as well as a critical evaluation of the effect of temperature, pH, Eh, substrate, and prior nutritional conditions of growth on enzymatic activity of selected species. Since cellulase is an adaptive enzyme in most fungi, the type of growth substrate becomes all the more critical in cellulolytic determinations. Possible correlations between amount of reproduction and degree of enzymatic activity need to be considered, for dissimilarities in RS production may be due to variation in reproduction of our cultures on different substrates. Such a relationship was described by Bose and Basu (1958) in species of *Chaetomium*.

Summary

1. Cellulolytic activity has been demonstrated in the following species of lignicolous marine Ascomycetes: *Lulworthia floridana* Meyers, *Torpedospora radiata* Meyers, *Ceriosporopsis halima* Linder, *Lignincola laevis* Höhnk, *Peritrichospora integra* Linder, and *Arenariomyces salinus* Meyers.

2. The Nelson-Somogyi method of reducing sugar determination was

used with insoluble (powered cellulose and balsa wood) and soluble (Sodium carboxymethylcellulose) celluloses as enzymic substrates.

3. Cell free filtrates of these fungi on cellulose and powdered balsa wood, under designated incubation conditions, produce approximately 0.075-0.150 mg reducing sugar (RS)/ml, with maximum RS production at less than 0.3 mg/ml.

4. Cellulolytic activity in the individual species studied varies considerably, as affected by such factors as the type and amount of substrate and the conditions of incubation.

5. Vegetative and reproductive development of the fungi, together with cellulolytic activity, occurs in sea water broth cultures, containing 0.1 per cent yeast extract and intact balsa wood slips.

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